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Editorial

In an era of increasing specialization in science, the generalist journal has become less common. We believe that such journals serve the important function of communicating research results from many disciplines, thereby enabling readers to be kept abreast of the latest advances in a number of specialities. However, a major disadvantage of the generalist journal is the difficulty in defining an editorial policy that presents clearly to potential authors the types of papers that will be accepted or rejected.

There has been considerable confusion recently concerning our conditions for acceptance or rejection. In previous editorials we have stated that the *Journal* wants the best manuscripts authors have to offer in the broad field of fisheries and aquatic sciences. However, what has not generally been appreciated is that *Journal* policy has evolved as the state of the art of various disciplines has progressed. For example, as strong foundations in some were established, the cutting edge of research shifted to experimental science, modeling, and holistic environmental studies. Consequently, editors accepted baseline or descriptive papers only in emerging disciplines, leaving some authors with the impression that decisions were arbitrary. Obviously a clearer, more precise definition of the *Journal*'s editorial policy was needed.

Accordingly, the first and second meetings of the Editorial Board were largely devoted to discussion of these matters. The statement that follows distills those discussions into a policy statement on what a *Journal* article should contain. By necessity it is broad, but we hope it clearly embodies the essential qualities of a *Journal* paper.

The *Canadian Journal of Fisheries and Aquatic Sciences* encourages papers dealing in general with the aquatic sciences, and in particular with fisheries and aquatic organisms. Papers may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and they should lead to identifiable conclusions or synthesis, which variously may amplify, modify, question or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. They should demonstrate clearly their contribution to knowledge beyond

Éditorial

À une époque où la spécialisation scientifique s'accentue, les journaux à vocation générale se font plus rares. Nous croyons que de tels journaux jouent un rôle important, celui de communiquer les résultats de recherches effectuées dans un grand nombre de disciplines, permettant ainsi aux lecteurs de se tenir au courant des tout derniers progrès réalisés dans un certain nombre de spécialités. Cependant, pour ce genre de journal, le grand inconvénient est la difficulté d'établir une politique de rédaction qui indique clairement aux auteurs éventuels les genres de textes qui seront acceptés ou refusés.

Dernièrement, il y a eu beaucoup de confusion au sujet des conditions que nous avons fixées pour accepter ou refuser des textes. Dans des éditoriaux précédents, nous avons indiqué que le *Journal* recherche les meilleurs manuscrits que les auteurs peuvent offrir dans le vaste domaine des sciences halieutiques et aquatiques. Cependant, de façon générale, les gens n'ont pas saisi que la politique du *Journal* a évolué au rythme des progrès réalisés dans les diverses disciplines. Par exemple, alors que des bases solides étaient établies dans certaines disciplines, la recherche de pointe s'est tournée vers la science expérimentale, la modélisation et les études environnementales holistiques. Par conséquent, les rédacteurs ont accepté des articles de fond ou des articles descriptifs uniquement dans de nouvelles disciplines, donnant l'impression à certains auteurs que les décisions étaient arbitraires. De toute évidence, il fallait redéfinir de façon plus précise et plus claire la politique de rédaction du *Journal*.

En conséquence, les deux premières réunions du Comité de rédaction ont porté en grande partie sur ces questions. Est sorti de ces discussions l'énoncé de principe suivant sur ce que devrait contenir un article de *Journal*. Cet énoncé est forcément général, mais nous espérons qu'il résume clairement les qualités essentielles que doit avoir un article publié dans le *Journal*.

Le *Journal canadien des sciences halieutiques et aquatiques* publie des textes qui portent de façon générale sur les sciences aquatiques et en particulier sur les organismes halieutiques et aquatiques. Les textes peuvent avoir trait aux cellules, aux organismes, aux populations, aux écosystèmes

the confirmatory state. Papers that apply standard techniques without breaking new methodological ground cannot be considered. Originality should relate to more than the particular (a certain year, place, taxon, or chemical compound) such that existing understanding is refined or reformulated.

It would assist the Editors if prospective authors identified briefly by covering letter, those aspects of their papers that in particular meet the foregoing objectives. Authors should recognize that clarity of intent and purpose of a paper, often well expressed in a covering letter to the Editor, also provides the same clarity to readers in general when suitably expressed in the introduction to a paper.

The *Journal* will continue to cover most disciplines in the aquatic sciences, thereby retaining its generalist orientation. We will encourage papers as just described and discourage those that have site-specific or local application, or confirm previously established principles. There must be an outer boundary to the *Journal*'s scope, however. Just because a paper concerns aquatic resources or reports research supported by the Federal Government does not automatically qualify it for consideration. For instance, theoretical physical oceanography, certain types of physical chemistry, waterfowl biology (unless it had a quantified impact on fish), and marine engineering are unsuitable disciplines for the *Journal*. Papers whose relevance to the *Journal*'s scope is debatable are sent to the Editorial Board for arbitration, with the benefit of doubt always given to the author.

We look forward to readers' responses to this Editorial, and as always, welcome any constructive comments.

J. WATSON
Editor-in-Chief

JOHANNA M. REINHART
Editor

ou aux processus qui influencent les systèmes de production aquatique et ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. Ils doivent clairement démontrer qu'ils contribuent aux connaissances en faisant plus que corroborer des faits. Les textes qui appliquent des techniques standard sans apporter des innovations méthodologiques ne peuvent être retenus. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles.

Les auteurs éventuels aideraient les rédacteurs s'ils identifiaient brièvement, dans une lettre d'accompagnement, les aspects de leurs textes qui répondent particulièrement aux objectifs indiqués ci-dessus. Les auteurs sont en outre priés de noter que l'objectif d'un article, bien exprimé dans une lettre d'accompagnement adressée au rédacteur, éclairera également le lecteur s'il est bien expliqué dans l'introduction.

Le *Journal* continuera à couvrir la plupart des disciplines qui font partie des sciences aquatiques, conservant ainsi son orientation généraliste. Nous favoriserons les articles répondant aux critères précités et rejèterons ceux qui se rapportent à un endroit en particulier ou qui ont une portée locale, ou encore qui ne font que corroborer des principes déjà établis. La portée du *Journal* doit cependant être limitée. Ce n'est pas parce qu'un document traite de ressources aquatiques ou relate des recherches appuyées par le Gouvernement fédéral qu'il sera automatiquement pris en considération. Par exemple, l'aspect théorique de l'océanographie physique, certains genres de chimie physique, la biologie des oiseaux aquatiques (à moins que ceux-ci aient un effet quantifié sur les poissons) et le génie maritime sont des disciplines qui ne conviennent pas au *Journal*. Les documents dont le rapport avec les objectifs du *Journal* est discutable sont envoyés au Comité de rédaction pour arbitrage, le bénéfice du doute étant toujours laissé à l'auteur.

Nous espérons recevoir les réactions des lecteurs à cet éditorial et, comme toujours, nous accueillerons avec plaisir toute critique constructive.

J. WATSON
Rédacteur en chef

JOHANNA M. REINHART
Rédactrice

Low pH and the Absence of Fish Species in Naturally Acidic Wisconsin Lakes: Inferences for Cultural Acidification

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RAHEL, F. J., AND J. J. MAGNUSON. 1983. Low pH and the absence of fish species in naturally acidic Wisconsin lakes: inferences for cultural acidification. Can. J. Fish. Aquat. Sci. 40: 3–9.

In a group of 138 northern Wisconsin lakes (pH 4.0–9.2), we observed differences in the lowest pH at which 31 fish species occurred. The central mudminnow (*Umbra limi*), yellow perch (*Perca flavescens*), and various centrarchids occurred below pH 5.0, whereas many cyprinids and darters were not found below pH 6.2. Rankings of species occurrence with minimum pH in these naturally acidic lakes were similar to data from Canadian lakes affected by acid precipitation, and rankings based on survival during laboratory exposure to low pH. Wisconsin oligotrophic lakes that are susceptible to acid precipitation typically lack many fish species sensitive to low pH, even when lake pH is near 7.0. Species interactions and biogeographic factors, not recent cultural acidification, are probably responsible for species absences in these lakes. Knowledge of the pH ranges naturally tolerated by fishes and the structure of fish assemblages in lakes sensitive to acid precipitation will aid in detecting changes caused by cultural acidification.

Key words: acid lake, acidification, pH, fish communities, Wisconsin

RAHEL, F. J., AND J. J. MAGNUSON. 1983. Low pH and the absence of fish species in naturally acidic Wisconsin lakes: inferences for cultural acidification. Can. J. Fish. Aquat. Sci. 40: 3–9.

Dans un groupe de 138 lacs du nord du Wisconsin (pH de 4,0–9,2), nous avons noté les différences de minimum de pH dans lesquels se trouvent 31 espèces de poissons. L'umbre de vase (*Umbra limi*), la perchaude (*Perca flavescens*) et divers centrarchidés se trouvent à des pH inférieurs à 5,0 tandis que plusieurs cyprinidés et dards ne se rencontrent pas à des pH inférieurs à 6,2. Si l'on classe les espèces habitant les pH les plus bas dans ces lacs naturellement acides, le schéma est identique (1) aux données recueillies dans les lacs canadiens exposés aux précipitations acides et (2) au classement fondé sur la survie après exposition à de bas pH en laboratoire. Les lacs oligotrophes du Wisconsin susceptibles de recevoir des précipitations acides sont typiquement dépourvus de plusieurs espèces de poissons sensibles à un bas pH, même proche de 7,0. L'absence d'espèces dans ces lacs est probablement due à des interactions interspécifiques et à des facteurs biogéographiques, plutôt qu'à de récentes acidification culturales. Les changements résultant de cette acidification seront détectés plus facilement si l'on connaît la fourchette des pH tolérés naturellement par ces poissons et la structure des groupements de poissons dans les lacs sensibles aux précipitations acides.

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DRAMATIC changes in the biota of lakes and streams coincident with declining pH and increasing metal concentrations have been linked to the occurrence of acidic precipitation in several parts of the world (Wright and Snekvik 1978; Harvey 1980; Cowling and Linthurst 1981). All trophic levels are affected, but the most visible and costly effect is the loss of entire fish populations from otherwise pristine waters (Hendrey et al. 1976; Pfeiffer and Festa 1980; Yan and Strus 1980). Because acid precipitation is becoming more widespread, the status of acid-sensitive fish species in lakes vulnerable to acidification is of growing interest (Cogbill 1976; Haines 1981). However, such studies are complicated by sparse information on the pH range naturally tolerated by most species, and the influence of biogeographic and limnological factors on species assemblages in these lakes.

To address the first problem, we examined fish assemblages in 138 northern Wisconsin lakes, many of which are naturally acidic. Some of these lakes are clearwater seepage lakes with pH values normally between 5.5 and 6.5, whereas others are brownwater bog lakes receiving acid inputs from surrounding peatlands and having pH values as low as 4.0. Both lake types occur elsewhere in the United States, but few

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TABLE 1. Lakes from which the 12 fish species used in the interspecific comparisons of acid tolerance were collected. All lakes are in Vilas County, Wisconsin. Further descriptions of the lakes are given in Rahel (1982) and Black et al. (1963). Species' scientific names are given in Fig. 1.

Species	Lake	pH[a]	Conductivity[a] (at 25°C)
Black bullheads	Grassy	6.8	85
Blacknose shiner	Grassy	6.8	85
Bluntnose minnow	Trout	7.6	63
Central mudminnow	Grassy	6.8	85
Common shiner	Trout	7.6	63
Golden shiner	Grassy	6.8	85
Mottled sculpin	Trout	7.6	63
Northern redbelly dace	Unnamed 8−9	6.1	13
Rock bass	Trout	7.6	63
Smallmouth bass	Trout	7.6	63
Walleye	Sparkling	7.8	73
Yellow perch	Trout	7.6	63

[a]Typical summer epilimnetic values.

studies have examined species occurrence in relation to hydrogen ion concentration (Hastings 1979; Kirk 1979; Patrick et al. 1981). Species distributions in relation to pH for these lakes were compared to similar data from areas affected by acid precipitation (Beamish 1976; Harvey 1980). Interspecific differences in acid sensitivity were also examined by comparing the survival of various species during exposure to a continuously decreasing pH in the laboratory.

To address the second problem, we compared fish assemblages in two types of lakes that differ in their sensitivity to acidification. In northern Wisconsin lakes, vulnerability to acidification is largely a function of hydrologic type. Seepage lakes lack surface-water connections to other water bodies and tend to be small and poorly buffered (Black et al. 1963). Hence these lakes are vulnerable to acidification. Drainage lakes tend to be larger and have higher alkalinities, making them less sensitive to acid inputs. Our goal was to relate fish community structure to a lake's biogeographic and limnological characteristics and to suggest species which should be monitored in lakes suspected of undergoing acidification.

Historical chemical data, some of which date back to the 1920s, document the occurrence of many naturally acidic lakes in northern Wisconsin (Juday et al. 1935; Black et al. 1963). In addition, recent studies have been unable to demonstrate decreases in pH since the 1930s in a set of northern Wisconsin lakes that includes 16 lakes considered in the present study (Bowser, Eilers, Gage, Horns, Magnuson, Rasmussen, University of Wisconsin, Madison, WI, personal communication). Thus, the observed fish distributions among these lakes should reflect conditions prior to major changes associated with cultural acidification.

Materials and Methods

Fish Species Distribution in Relation to Lake pH

Fish species lists and limnological data were assembled for 138 northern Wisconsin lakes. Details on individual lakes and references for all data sources are given in Rahel (1982, Appendix II). We sampled 51 lakes during the summer months of 1979−81, and obtained data on the remaining lakes from records of the Wisconsin Department of Natural Resources (Woodruff, WI) and from student theses done at the University of Wisconsin. All lakes had been sampled with at least one type of gear appropriate for small fishes [minnow traps, seines, or small-mesh (5-mm square) fyke nets] and at least one type of gear appropriate for larger species (electroshocking, gill nets, trammel nets, or large-mesh fyke nets). The 138 lakes were selected from a larger set and represent lakes which, in our judgment, had been sufficiently sampled so that fish species lists are reasonably accurate. Sampling effort did vary among lakes; hence we restricted our analyses to presence/absence data. The lowest pH at which each species occurred was based on the occurrence of populations in several lakes at or near the indicated pH.

For the lakes that we sampled, which includes most of the acidic lakes, water chemistry measurements are summer values for samples collected in a 1-L polyethylene bottle at a depth of 0.25 m near the middle of the lake. We measured pH (Orion 407A pH meter), conductivity (Montedoro-Whitney CTU-3B conductivity meter), and alkalinity (potentiometric, low-alkalinity method, APHA 1976). Measurements were made in the field, or in the laboratory within several hours of sample collection. Most lakes were sampled two or three times, with the lowest pH value used in the analysis of species distributions in relation to lake pH. Chemical data for the other lakes are epilimnetic summer values and were obtained from the same sources as the fish survey records (Rahel 1982).

Laboratory Comparison of pH Tolerance Among Fish Species

Twelve fish species were collected from nonacidic lakes (pH > 6.0) in Vilas County, Wisconsin, during August 1980 (Table 1). Fish were captured with fyke nets or by seining and allowed to acclimate for 24−72 h to unacidified Trout Lake water at 19°C (pH 7.6, alkalinity 27 mg/L $CaCO_3$, conductivity 77 μs, sodium 0.07 mmol/L, calcium 0.14 mmol/L). Exposure to low pH (as sulfuric acid) was done in a 2000-L tank with a flow-through rate of 180 L per hour. All species were tested simultaneously in the same tank. Some species were isolated in nylon net cages, which allowed water exchange but prevented predation on the smaller species. The pH was lowered from ambient to 5.5 during the first 24 h of the bioassay, then by 0.5 pH units per day during days 2−4. After day four, the pH was lowered ~0.2 units/d until the end of the experiment. Observations were made at least every 6 h, with survival time and wet weight recorded for each fish when opercular movement stopped.

Young-of-the-year of four species were tested along with adults. These young fish were similar in size to the cyprinid species tested (Table 2). By comparing the survival of similar sized fish, interspecific differences in acid tolerance could be evaluated apart from size influences (Spry et al. 1981).

Fish Assemblages in Lakes Vulnerable to Acidification

Two types of lakes, differing in their vulnerability to acid-

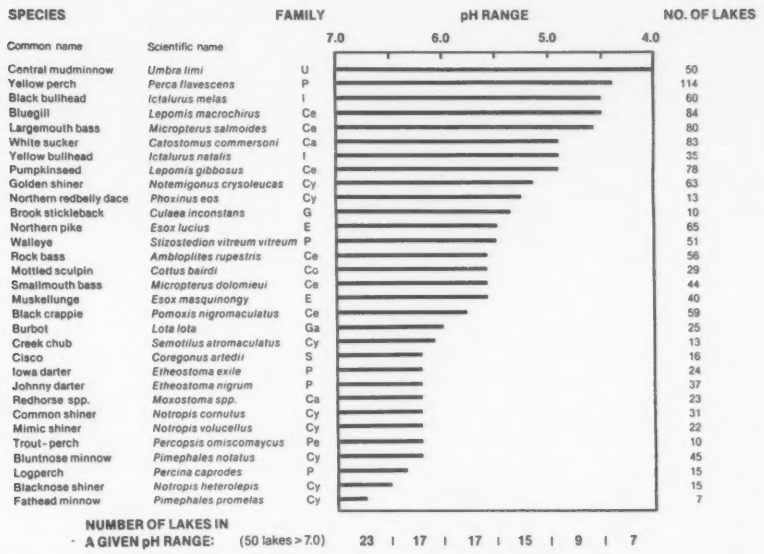
SPECIES
FAMILY
pH RANGE
NO. OF LAKES
7.0
6.0
5.0
4.0
Common name
Scientific name
Central mudminnow Umbra limi U 50
Yellow perch Perca flavescens P 114
Black bullhead Ictalurus melas I 60
Bluegill Lepomis macrochirus Ce 84
Largemouth bass Micropterus salmoides Ce 80
White sucker Catostomus commersoni Ca 83
Yellow bullhead Ictalurus natalis I 35
Pumpkinseed Lepomis gibbosus Ce 78
Golden shiner Notemigonus crysoleucas Cy 63
Northern redbelly dace Phoxinus eos Cy 13
Brook stickleback Culaea inconstans G 10
Northern pike Esox lucius E 65
Walleye Stizostedion vitreum vitreum P 51
Rock bass Ambloplites rupestris Ce 56
Mottled sculpin Cottus bairdi Co 29
Smallmouth bass Micropterus dolomieui Ce 44
Muskellunge Esox masquinongy E 40
Black crappie Pomoxis nigromaculatus Ce 59
Burbot Lota lota Ga 25
Creek chub Semotilus atromaculatus Cy 13
Cisco Coregonus artedii S 16
Iowa darter Etheostoma exile P 24
Johnny darter Etheostoma nigrum P 37
Redhorse spp. Moxostoma spp. Ca 23
Common shiner Notropis cornutus Cy 31
Mimic shiner Notropis volucellus Cy 22
Trout-perch Percopsis omiscomaycus Pe 10
Bluntnose minnow Pimephales notatus Cy 45
Logperch Percina caprodes P 15
Blacknose shiner Notropis heterolepis Cy 15
Fathead minnow Pimephales promelas Cy 7
NUMBER OF LAKES IN A GIVEN pH RANGE: (50 lakes > 7.0) 23 | 17 | 17 | 15 | 9 | 7

FIG. 1. The distribution of 31 fish species in relation to pH for 138 northern Wisconsin lakes. Family names are abbreviated as follows: Catostomidae (Ca), Centrarchidae (Ce), Cottidae (Co), Cyprinidae (Cy), Esocidae (E), Gadidae (Ga), Gasterosteidae (G), Ictaluridae (I), Percidae (P), Percopsidae (Pe), Salmonidae (S), Umbridae (U).

ification, were selected from the 138 lakes. All were non-bog lakes that did not become anoxic in winter and had summer pH values above 5.0. One group consisted of lakes most sensitive to acidification: seepage lakes characterized by small size (<0.8 km^2), low alkalinity (≤15 mg/L $CaCO_3$), and a lack of inlet/outlet streams. Their low alkalinities provide little capacity for neutralizing incoming acids, whereas small size and isolation are biogeographic factors known to limit species diversity (MacArthur and Wilson 1967; Magnuson 1976). The value of 15 mg/L $CaCO_3$ was based on a study of northern Wisconsin lakes which suggested that waters below this alkalinity are the most susceptible to acidification (Glass 1980). The second group consisted of drainage lakes with alkalinities above 15 mg/L $CaCO_3$. Comparing fish assemblages in these two lake types should provide insights into the factors influencing which fish species are typically present, and which are typically absent, in midwestern lakes sensitive to acidification.

Results

Fish Species Distributions in Relation to Lake pH

Differences were evident in the occurrence of species in relation to pH (Fig. 1). Darters and most cyprinids were absent below pH 6.2, whereas black bullheads (*Ictalurus melas*), yellow perch (*Perca flavescens*), and several centrarchids occurred below pH 5.0. The central mudminnow (*Umbra limi*) occurred at the lowest pH, inhabiting bog drainage channels at a pH of 4.0.

The lowest pH at which 13 species occurred in our sampling is similar to the lowest pH at which these species appeared unaffected in Canadian lakes affected by acid precipitation (Harvey 1980) (Fig. 2). Species surviving at low pH in culturally acidified lakes are the same ones inhabiting lakes which are naturally acidic.

Laboratory Comparisons of pH Tolerance Among Fish Species

In the laboratory, cyprinids were the most sensitive to declining pH, while yellow perch, central mudminnows, and black bullheads were the most acid-tolerant (Table 2). Tolerance rankings were similar to those based on distributions in 138 northern Wisconsin lakes (Fig. 1, Spearman's rank correlation coefficient $r_s = 0.85$, $P < 0.01$). Young-of-the-year fish had median survival times similar to the adults tested. Young perch and black bullheads were of comparable size to the cyprinids tested, but survived much longer. Hence the acid intolerance of these cyprinids is not merely due to their small size, but reflects their greater physiological sensitivity to acid stress.

Fish Assemblages in Lakes Vulnerable to Acidification

Differences in the fish species assemblages of the two lake types were evident (Table 3). Although almost all lakes in both groups contained yellow perch, white suckers, and various centrarchids, the lakes most sensitive to cultural acidification frequently lacked minnows, darters, and mottled

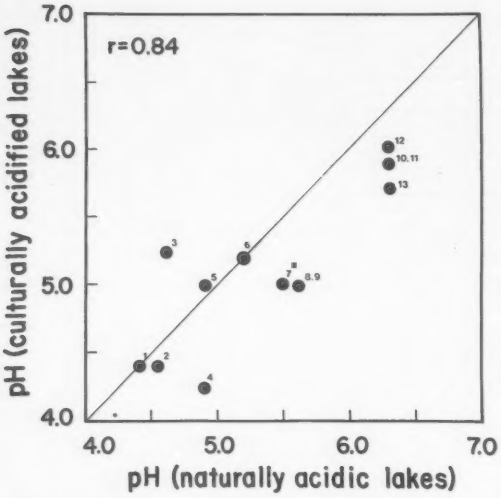

FIG. 2. Lowest pH at which fish species appeared unaffected in culturally acidified lakes (Harvey 1980) compared to the lowest pH at which they occurred in naturally acidic lakes (present study). The diagonal line separates species occurring at a lower pH in naturally acidic lakes (above diagonal) from those that occur at a lower pH in culturally acidified lakes (below diagonal). Species are numbered as follows:

1. Yellow perch
2. Bluegill
3. Largemouth bass
4. Pumpkinseed
5. White sucker
6. Golden shiner
7. Northern pike
8. Rock bass
9. Smallmouth bass
10. Iowa darter
11. Johnny darter
12. Bluntnose minnow
13. Common shiner

The regression equation is $Y = 1.40 + 0.69\,(X)$; the slope is significantly less than one ($t_{11} = 2.28$, $P < 0.05$).

sculpins (*Cottus bairdi*). These are the taxa most sensitive to low pH based on their distribution in naturally acidic waters (Fig. 1), their low survival times in the laboratory bioassay (Table 2), and their early disappearance in lakes affected by acid precipitation (Harvey 1980). Some lakes most vulnerable to acid precipitation have pH values naturally below 6.2, and therefore the absence of certain species in these lakes could be attributed to physiological stress. However, 10 of the 25 lakes have pH values above 6.2 and the absence of cyprinids, darters, and sculpins in these lakes cannot be attributed to low pH.

Discussion

The distribution of fish species among northern Wisconsin lakes suggests major interspecific differences in acid tolerance. Many species of cyprinids and darters appear to be highly acid-sensitive and were not found below pH 6.2. Taxa that are quite tolerant of acid conditions include the central mudminnow, yellow perch, black bullhead, and several centrarchids.

However, it is difficult to infer species differences in acid sensitivity solely from distributional data because pH is correlated with other factors. For example, naturally acid lakes in northern Wisconsin tend to be small, shallow, and have no inlet or outlet streams. Salmonids would not be expected in these lakes because there is no cool, well-oxygenated hypolimnion to provide summer habitat. Fortunately, it is possible to isolate the effects of pH in some cases. For example, cyprinids were generally absent from small seepage lakes initially examined during this study (Rahel 1982). The habitat of these lakes appeared suitable for cyprinids, and we could not determine whether their absence was caused by low pH or by predation/competition from centrarchid species. The question was resolved by our sampling lakes that experience winter anoxia, which is known to eliminate centrarchids and favor the establishment of cyprinid assemblages (Tonn and Magnuson 1982). In these lakes, some cyprinid species [e.g. northern redbelly dace (*Phoxinus eos*), golden shiner (*Notemigonus crysoleucas*)] were abundant above pH 5.2–5.4, but were not found below pH 5.2. Thus, for these species, a pH below 5.2 appears to be a limiting factor (Rahel 1982).

Lower pH limits inferred from our distributional data agree with lower "safe" pH limits established through laboratory bioassays or by experimental manipulations of lake pH. For example, Mount (1973) found reproduction in fathead minnows to be reduced at pH 6.6 and lower during a 13-mo exposure involving all life history stages. The lowest safe pH for white suckers appears to be near 5.0 as reproduction was severely impaired below this pH (Trojnar 1977) and adults stopped feeding in the pH range 4.5–5.0 (Beamish 1972). These values are similar to the lowest pH at which we found fathead minnows (pH 6.8) and white suckers (pH 4.9). In an experimental acidification of a Canadian Shield lake, fathead minnows were abundant above pH 6.7, but approached extinction as pH fell below 6.0 (Schindler et al. 1980; Mills 1982). In the same lake, white suckers experienced reproductive impairment around pH 5.1. In the New Jersey Pine Barrens, largemouth bass (*Micropterus salmoides*) and pumpkinseeds (*Lepomis gibbosus*) were regularly stocked into a brownwater lake (pH 4.1–4.5), but no reproduction occurred until the pH was raised above 4.5 by liming (Smith 1957). This agrees with the absence of largemouth bass below pH 4.6 and pumpkinseeds below pH 4.9 in northern Wisconsin lakes. As with laboratory bioassays, however, experimental manipulations have provided data on only a few fish species.

Our results are also generally consistent with the few published studies of fish distributions in other naturally acidic waters. Acidic streams in the New Jersey Pine Barrens are dominated by centrarchids and generally lack cyprinids despite the potential for colonization by downstream populations (Smith 1957; Hastings 1979). Except for the ironcolor shiner, *Notropis chalybaeus*, cyprinids were also absent from dystrophic North Carolina lakes (pH 4.3–4.9) (Frey 1951).

The relative acid tolerance of species determined in the present study (Tables 2 and 3) is consistent with the order of species disappearance in culturally acidified lakes of the LaCloche Mountains, Ontario (Beamish 1976). Smallmouth bass (*Micropterus dolomieui*), walleye (*Stizostedion vitreum vitreum*), and burbot (*Lota lota*) were thought to have stopped reproducing in the pH range 5.5–6.0, which is similar to the lowest pH at which naturally reproducing populations were found in northern Wisconsin lakes (Fig. 1). The tendency for

TABLE 2. The survival of 12 fish species simultaneously exposed to a continuously declining pH. Young-of-the-year of four species were also tested. Species are ranked from most sensitive to least sensitive based on median survival time of adults. Tolerance rankings based on field distribution (Fig. 1) are included for comparison. Species' scientific names are given in Fig. 1.

	N	Survival time (h) median (range)	pH at median survival time	% alive at termination	Wet wt (g) mean (range)	Sensitivity rank based on: laboratory survival	Sensitivity rank based on: field distribution
Blacknose shiner	28	99 (89–111)	4.05	0	1.5 (1–2.4)	1	1
Bluntnose minnow	15	105 (65–111)	4.00	0	3.7 (2.4–5.5)	2.5	2.5
Common shiner	25	105 (65–117)	4.00	0	8.7 (4.7–15)	2.5	2.5
Northern redbelly dace	23	126 (123–140)	3.85	0	1.5 (0.7–2)	4	8
Smallmouth bass	12	160 (135–162)	3.60	0	29.0 (3–57)	5	5
Mottled sculpin	24	162 (142–174)	3.55	0	1.0 (0.4–4.5)	6	5
Golden shiner (young)	24	174 (41–180)	3.45	0	0.6 (0.3–1.4)	—	—
Golden shiner (adult)	18	176 (160–186)	3.45	0	8.6 (3.0–17.3)	7	9
Walleye	11	220 (32–>240)	3.20	18	36.0 (8–123)	8	7
Rock bass (adult)	21	223 (198–>240)	3.15	14	40.0 (14–79)	9	5
Black bullhead (young)	31	223 (198–>240)	3.15	3	1.2 (0.6–2.7)	—	—
Rock bass (young)	29	236 (200–>240)	3.10	31	2.7 (1.7–3.6)	—	—
Black bullhead (adult)	25	240 (180–>240)	3.05	48	10.4 (5.8–15.2)	10.5	10
Central mudminnow	17	240 (138–>240)	3.05	41	4.7 (2.5–10)	10.5	12
Yellow perch (young)	25	>240 (234–>240)	<3.05	96	1.1 (0.8–2.4)	—	—
Yellow perch (adult)	25	>240 (65–>240)	<3.05	80	15.0 (9–22)	12	11

some species to occur at lower pH values in culturally acidified lakes than in naturally acidic lakes (Fig. 2) has two explanations. Lower pH limits inferred from culturally acidified lakes may be too high as some species might have already stopped reproducing but still be present in a lake (Harvey 1980). Alternatively, our limits may be too high, as some species may have been absent from acidic Wisconsin lakes because other habitat factors were unsuitable. This would appear to be especially true for species that prefer larger lakes and rock or gravel substrates. Many naturally acidic Wisconsin waters are brownwater lakes which tend to be small and lack such substrates (Rahel 1982). For example, rock bass (*Ambloplites rupestris*) occur at lower pH values in culturally acidified lakes having firm bottom substrates, than in muck-bottom, naturally acidic lakes (Ryan and Harvey 1977).

Many species of cyprinids and darters, as well as the mottled sculpin, would be sensitive indicators of lake acidification. Unfortunately, these species are generally absent from those Wisconsin lakes likely to be the first affected by acid precipitation (i.e. the seepage lakes, Table 3). Because some low alkalinity lakes naturally have pH values below 6.0, these lakes may have always been too acidic for certain taxa. Yet even many neutral pH lakes lacked cyprinids, darters, and mottled sculpins, suggesting that biotic interactions are important in determining species composition. Their absence from small unproductive lakes with abundant centrarchid populations has been observed by others (Jewell and Brown 1929; Rubec 1975), even after they have been stocked (Rahel 1982). In our study area, Tonn and Magnuson (1982) also reported the absence of these taxa in small lakes dominated by centrarchids. They suggested that predation and competition from centrarchids and northern pike eliminates small-bodied, soft-rayed species such as cyprinids from small, oligotrophic lakes. Thus, the absence of many acid-sensitive species from Wisconsin lakes vulnerable to cultural acidification may result from biotic interactions.

Isolating the effects of water chemistry on fish assemblages would require a comparison among lakes of similar size and hydrology, but differing sensitivity to acidification. Although this was not possible with our data set, Wiener et al. (1982) have recently made such a comparison involving 12 small, northern Wisconsin, seepage lakes that differ mainly in pH-related chemical characteristics. Cyprinids, darters, and mottled sculpins were absent from the six lakes sensitive to acidification. A few species of minnows and darters were present in the six lakes not vulnerable to acidification, but even these circumneutral pH lakes lacked many of the species present in large drainage lakes. Thus, biogeographic factors (small size, lack of inlets/outlets) and biotic interactions probably contribute to the absence of minnows, darters, and mottled sculpins in Wisconsin lakes that are highly vulnerable to cultural acidification.

The ubiquity of centrarchids and yellow perch, and the almost complete absence of small prey species in low-alkalinity lakes, indicate that this community structure is a predictable characteristic of small, oligotrophic lakes in northern Wisconsin. This community structure should have also characterized the study lakes in their recent past and should not, therefore, be cited as evidence for the recent acidification of Wisconsin lakes. Whether the absence of small prey species is characteristic of lakes sensitive to acidification but not dominated by centrarchids is unknown. It may not, however, because oligotrophic lakes in northwestern Ontario, Canada, that lack centrarchids frequently contain low-pH sensitive taxa missing from oligotrophic Wisconsin lakes (Beamish et al. 1976). This is probably because different predator species dominate these colder-water Ontario lakes. These lakes also have inlet/outlet streams which could provide refuges from predators and colonization corridors should local extinctions occur (Moyle 1973).

Smallmouth bass, black crappie (*Pomoxis nigromaculatus*), and golden shiner may be among the best species to

TABLE 3. Comparison of fish species composition and limnological parameters among lakes differing in their sensitivity to acid precipitation. Lakes least sensitive to acidification are drainage lakes with alkalinities above 15 mg/L $CaCO_3$. Lakes most sensitive are small (≤0.8 km^2) seepage lakes with alkalinities ≤15 mg/L $CaCO_3$. All lakes have summer pHs above 5.0 and are not anoxic in winter. Species' scientific names are given in Fig. 1.

	% of lakes with a given taxon	
	Lakes least sensitive to acidification $n = 41$	Lakes most sensitive to acidification $n = 25$
Taxa commonly found[a] *in both lake types*		
Catostomidae		
White sucker	100	68
Centrarchidae		
Largemouth bass	88	80
Lepomis spp.	100	92
Ictaluridae		
Ictalurus spp.	83	52
Percidae		
Yellow perch	100	96
Taxa uncommon in lakes sensitive to acidification		
Catostomidae		
Moxostoma sp.	49	0
Centrarchidae		
Smallmouth bass	61	24
Rock bass	85	20
Black crappie	90	40
Cottidae		
Mottled sculpin	54	4
Cyprinidae		
Golden shiner	85	32
Notropis spp.	76	4
Pimephales spp.	73	8
Esocidae		
Esox spp.	98	40
Gadidae		
Burbot	49	4
Percidae		
Walleye	88	12
Etheostoma or *Percina* spp.	81	4

	Limnological variables[b]	
Lake size (km^2)	2.1 (0.10–15.7)	0.2 (0.04–0.7)
pH	7.2 (6.3–8.6)	6.2 (5.2–8.1)
Alkalinity (mg/L $CaCO_3$)	36 (17–120)	4.3 (0.5–15)
Number of fish species	18 (10–33)	6.8 (4–14)

[a]Defined as occurring in 50% or more of lakes in a given category.
[b]All values are mean (range) except pH which is median (range).

monitor in Wisconsin lakes that are vulnerable to cultural acidification. They are moderately common in this lake type (Table 3) and are fairly sensitive to low pH (Fig. 1; Beamish 1976). Cyprinid and darter populations in small, shallow, low-alkalinity, seepage lakes would be very sensitive to acidification, but population fluctuations due to winter anoxia would have to be taken into account before changes due to acidification could be detected.

In summary, pH tolerances based on species distributions in naturally acidic lakes generally agree with limits determined from long-term laboratory bioassays, field manipulations of pH, and species disappearances in lakes affected by acid precipitation. The discrepancies which occurred were generally minor, involving only a few tenths of a pH unit, or could be explained by consideration of a species' autecology. Although safe limits should ideally be corroborated by long-term, laboratory bioassays involving all life history stages, such studies are expensive and time-consuming and have so

far produced data for only a few species (Haines 1981; Spry et al. 1981). Our data allow predictions of the relative acid sensitivity of many common fish species, and indicate the species assemblages typical of low-alkalinity, midwestern lakes vulnerable to acid precipitation.

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BEAMISH, R. J. 1972. Lethal pH for the white sucker (*Catostomus commersoni*). Trans. Am. Fish. Soc. 101: 355–358.

1976. Acidification of lakes in Canada by acid precipitation and the resulting effects on fishes. Water Air Soil Pollut. 6: 501–514.

BEAMISH, R. J., L. M. BLOUW, AND G. A. MCFARLANE. 1976. A fish and chemical study of 109 lakes in the Experimental Lakes Area (ELA), northwestern Ontario, with appended reports on lake whitefish aging errors and the northwestern Ontario baitfish industry. Fish. Mar. Serv. Can. Tech. Rep. 607.

BLACK, J. J., L. M. ANDREWS, AND C. W. THREINEN. 1963. Surface water resources of Vilas County. Wisconsin Conservation Department, Madison, WI.

COGBILL, C. V. 1976. The history and character of acid precipitation in eastern North America. Water Air Soil Pollut. 6: 407–413.

COWLING, E. B., AND R. A. LINTHURST. 1981. The acid precipitation phenomenon and its ecological consequences. Bioscience 31: 649–654.

FREY, D. G. 1951. The fishes of North Carolina's bay lakes and their intraspecific variation. J. Elisha Mitchell Sci. Soc. 67: 1–44.

HAINES, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. Trans. Am. Fish. Soc. 110: 669–707.

HARVEY, H. H. 1980. Widespread and diverse changes in the biota of North American lakes and rivers coincident with acidification, p. 93–98. *In* D. Drablos and T. Tollan [ed.] Proceedings of the International Conference on the Ecological Impact of Acid Precipitation. Acid precipitation-effects on forest and fish project, Norway.

HASTINGS, R. W. 1979. Fish of the Pine Barrens, p. 489–504. *In* R. T. T. Forman [ed.] Pine Barrens: ecosystem and landscape. Academic Press, New York, NY.

HENDREY, G. R., K. BAALSRUD, T. S. TRAAEN, M. LAAKE, AND G. RADDUM. 1976. Acid precipitation: some hydrobiological changes. Ambio 5: 224–227.

JEWELL, M. E., AND H. W. BROWN. 1929. Studies on northern Michigan bog lakes. Ecology 10: 427–475.

JUDAY, C., E. A. BIRGE, AND V. W. MELOCHE. 1935. The carbon dioxide and hydrogen ion content of the lake waters of northeastern Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 31: 223–276.

KIRK, P. W. JR. [ed.]. 1979. The great dismal swamp. Old Dominion University Research Foundation Inc., University of Virginia Press, Charlottesville, VA.

MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

MAGNUSON, J. J. 1976. Managing with exotics — a game of chance. Trans. Am. Fish. Soc. 105: 1–9.

MILLS, K. H. 1982. Fish population responses during the experimental acidification of a small lake. *In* G. R. Hendrey [ed.] Chronic stress of acidification on freshwater biota: pH 5 to 6. Am. Chem. Soc. Symp. Ser., Ann Arbor Science Publishers, Ann Arbor, MI. (In press)

MOUNT, D. I. 1973. Chronic effect of low pH on fathead minnow survival, growth and reproduction. Water Res. 7: 987–993.

MOYLE, P. B. 1973. Ecological segregation among three species of minnows (Cyprinidae) in a Minnesota lake. Trans. Am. Fish. Soc. 102: 794–805.

PATRICK, R., V. P. BINETTI, AND S. G. HALTERMAN. 1981. Acid lakes from natural and anthropogenic causes. Science 211: 446–448.

PFEIFFER, M. H., AND P. J. FESTA. 1980. Acidity status of lakes in the Adirondack region of New York in relation to fish resources. N.Y. State Dep. Environ. Conserv. Rep. FW-P168, Albany, New York.

RAHEL, F. J. 1982. Fish assemblages in Wisconsin bog lakes. Ph.D. thesis, University of Wisconsin, Madison, WI.

RUBEC, P. J. 1975. Fish distribution in Gatineau Park, Quebec, in relation to postglacial dispersal, man's influence, and eutrophication. Can. Field-Nat. 89: 389–399.

RYAN, P. M., AND H. H. HARVEY. 1977. Growth of rock bass, *Ambloplites rupestris*, in relation to the morphoedaphic index as an indicator of an environmental stress. J. Fish. Res. Board Can. 34: 2079–2088.

SCHINDLER, D. W., R. WAGEMANN, R. B. COOK, T. RUSZCZYNSKI, AND J. PROKOPOWICH. 1980. Experimental acidification of Lake 223, Experimental Lakes Area: background data and the first three years of acidification. Can. J. Fish. Aquat. Sci. 37: 342–354.

SMITH, R. F. 1957. Lakes and ponds. Fish. Surv. Rep. No. 3. N.J. Dep. Conserv. Econ. Develop. Div. Fish Game, Trenton, NJ.

SPRY, D. J., C. M. WOOD, AND P. V. HODSON. 1981. The effects of environmental acid on freshwater fish with particular reference to the softwater lakes in Ontario and the modifying effects of heavy metals. A literature review. Can. Tech. Rep. Fish. Aquat. Sci. No. 999.

TONN, W. M., AND J. J. MAGNUSON. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63: 1149–1166.

TROJNAR, J. R. 1977. Egg and larval survival of white suckers (*Catostomus commersoni*) at low pH. J. Fish. Res. Board Can. 34: 262–266.

WIENER, J. G., P. J. RAGO, AND J. M. EILERS. 1982. Species composition of fish communities in northern Wisconsin lakes: relation to pH. *In* G. R. Hendrey [ed.] Chronic stress of acidification on freshwater biota: pH 5 to 6. American Chemical Society Symposium Series, Ann Arbor Science Publishers, Ann Arbor, MI. (In press)

WRIGHT, R. F., AND E. SNEKVIK. 1978. Acid precipitation: chemistry and fish populations in 700 lakes in southernmost Norway. Ver. Int. Verein. Limnol. 20: 765–775.

YAN, N. D., AND R. STRUS. 1980. Crustacean zooplankton communities of acidic metal-contaminated lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 37: 2282–2293.

Error Bounds for Estimates of Entrained Ichthyoplankton[1]

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MADENJIAN, C. P., AND D. J. JUDE. 1983. Error bounds for estimates of entrained ichthyoplankton. Can. J. Fish. Aquat. Sci. 40: 10–16.

Entrainment of fish larvae and eggs was monitored at the J. H. Campbell Plant, eastern Lake Michigan, from 1977 to 1979. A procedure for calculating error bounds for estimated number of fish larvae (or eggs) entrained by the plant for each year of operation, assuming independence among observations, was outlined. A new method for calculating these bounds was devised by adjusting the variance for its non-independent component, using time series analysis. Serial correlation in the data was accounted for by modeling the sequence of entrainment data for a year as a time series. For many taxa of fish larvae the entrainment observations were determined to be independent and no adjustment was necessary. The width of the adjusted error-bound intervals ranged from 4.8 to 87.9% greater than unadjusted ones for those taxa for which adjustment was required, thus assuming independence among observations could result in serious underestimation of the error-bound interval.

Key words: error bounds, variance, entrainment, Lake Michigan, serial correlation, time series analysis

MADENJIAN, C. P., AND D. J. JUDE. 1983. Error bounds for estimates of entrained ichthyoplankton. Can. J. Fish. Aquat. Sci. 40: 10–16.

On a surveillé, de 1977 à 1979, la quantité de larves et d'oeufs de poissons entraînés par les eaux à la centrale J. H. Campbell, dans la partie est du lac Michigan. Le présent rapport esquisse une méthode de calcul des limites d'erreur du nombre estimatif de larves (ou d'oeufs) de poissons entraînés par les eaux de la centrale au cours de chaque année d'exploitation, en supposant que les observations sont indépendantes. Une nouvelle méthode de calcul de ces limites a été conçue en ajustant le composant non indépendant de la variance à l'aide d'une analyse par séries chronologiques. La corrélation en série des données est justifiée par la modélisation de la séquence des données annuelles en une série chronologique. On a déterminé que, pour un grand nombre de taxons de larves de poisson, les observations sont indépendantes et aucune mise au point n'est nécessaire. Les intervalles ajustés des limites d'erreur varient de 4,8 à 87,9 % de plus que ceux non ajustés pour les taxons qui nécessitent une mise au point. Ainsi, une sous-estimation importante de l'intervalle de la limite d'erreur peut résulter lorsqu'on suppose que les observations sont indépendantes.

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ONE of the objectives of an environmental impact study for a power plant drawing cooling water from a lake, river, or ocean is to estimate the total number of fish larvae and fish eggs entrained by the plant during its annual operation. Although a seemingly simple procedure, such estimates are complicated because relatively small sample volumes are taken, variability is high, and samples may not be independent. Bounds on the error for these estimates are desirable, as they allow one to make probabilistic statements about the magnitude of the impact. The purpose of this paper is to present a new method for estimating numbers of fish larvae and eggs entrained and for calculating bounds for the estimates. The method explicitly accounts for the lack of independence among observations by adjusting the variance for its non-independent component.

Entrainment estimates have been discussed by other researchers (Jude 1975; Snyder 1976; Teleki 1976) but in most cases estimates were for 24-h periods and not for the entire year. Variances for the estimates were rarely discussed and when presented, were for the 24-h period. In calculating variances for yearly projections, the problem of non-independence in observations between 24-h sampling periods should be addressed. This paper focuses on calculations of error bounds for yearly entrainment estimates using a time series technique to deal with the problem of non-independence in observations.

In applying this technique it is useful to regard non-independence among the 24-h period entrainment obser-

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vations as serial correlation. Serial correlation may be interpreted as redundancy or replication of information from one observation to the other (Loftis and Ward 1980). A sample of observations taken from a certain population at different times will contain less information if the observations are serially correlated than if they are uncorrelated. The method of accounting for serial correlation involves a branch of statistics known as time series analysis.

The correction for serial correlation includes a variance adjustment. The basic principle of the variance adjustment is illustrated by the following example. If two random variables X and Y are independent then the variance for their sum, $V(X + Y)$, is equal to the sum of the variances, $V(X) + V(Y)$. However, if X and Y are not independent then the variance of the sum is equal to

$$V(X + Y) = [V(X) + V(Y)] + [2\mathrm{Cov}(X, Y)]$$

where $\mathrm{Cov}(X, Y)$ is the covariance between X and Y. Thus the quantity $V(X + Y)$ can be separated into two components. We shall refer to the covariance term as the dependent or non-independent component of the variance, whereas the sum of the variances, $V(X) + V(Y)$, is labeled the independent component of the variance, $V(X + Y)$. Time series analysis allows for assessment of the non-independent component of a variance of a sum of serially correlated random variables.

Important tools of time series analysis are the correlogram and the estimated partial autocorrelation function of the time series data. The correlogram is the estimated autocorrelation function, i.e. the set of estimated correlations between the time series value at time t and the value k steps before time t with k varying from 1 to K (K usually is chosen as 20). The estimated partial autocorrelation function (estimated p.a.c.f.), analogous to the case of multiple linear regression, is the set of estimated correlations between the time series value at time t and the value at time $t - k$, taking into account the effects of the time series values from time $t - 1$ to time $t - k + 1$, for k varying from 1 to K.

Entrainment Sampling Procedures

Entrainment sampling was performed at the J. H. Campbell Plant, eastern Lake Michigan, from 1977 through 1979 with 0.5-m-diameter plankton nets with No. 2 (363-μm aperture) mesh and a flowmeter attached to the frame at the mouth of the net to determine volume of water filtered (Jude et al. 1980). The net was suspended in the discharge canal of the plant so that it was completely submerged. Because the current in the discharge canal was strong, an 18-kg weight was tied to the net to keep it submerged. The net was suspended in the water for 10 min, retrieved, and then washed down thoroughly. Contents of the sample were placed into a 0.473-L glass jar and ~40 mL of formaldehyde was added for preservation. Samples were examined under binocular microscopes and fish larvae were identified and counted; fish eggs were also counted but were not identified to species. Fish larvae were arbitrarily defined as any fish less than or equal to 25.4 mm in length. Larger fish were considered fry.

Entrained ichthyoplankton were sampled during a 24-h period about once a week. The 24-h period was divided into the following diel periods: dawn, day, dusk, and night. Within each diel period sampled, four replicate samples, each one 10 min in duration, were taken. In 1977, sampling was conducted for the day and night diel periods only; however, beginning in spring 1978 and continuing through 1979, dawn and dusk samples were also collected. Thus, during most of 1978 and throughout 1979, 16 samples were taken during every 24-h sampling period. During winter 1979, sampling was somewhat reduced with entrained ichthyoplankton sampled twice a month in January, February, and December.

Estimation Assuming Independence Among Observations

Each diel period sampled was assigned a duration time (number of hours) by using times for sunrise and sunset obtained from the Nautical Almanac Office, U.S. Naval Observatory, Washington, DC. The dawn and dusk periods were defined as those periods 1 h before and 1 h after sunrise and sunset, respectively. The day period was the period between the end of dawn and the beginning of the dusk period, and the night period was assigned the remainder of the 24 h. In those cases when only day and night samples were taken, the day period was assigned the hours between sunrise and sunset, whereas the night period included the rest of the 24 h.

Flow rate of water through the plant was obtained from the power plant engineers. Estimated number of larvae or eggs entrained for diel period i for sampling period j was equal to the product of the flow rate f_j, the hours assigned that diel period h_{ij}, and the average density $\bar{C}_{ij}$ for a particular taxon of larvae or for eggs. Thus, the number for a particular taxon of larvae or of eggs estimated entrained for a 24-h period, N_j, was equal to the sum of the products of these three quantities for all diel periods sampled during the 24-h period:

$$N_j = f_j \sum_{i=1}^{d_j} h_{ij}\, \bar{C}_{ij}$$

where:

f_j = flow rate (1000 m^3/h) for sampling period j, $j = 1, \ldots, n$

n = number of 24-h sampling periods for the entire year

d_j = number of diel periods sampled for 24-h period j, $j = 1, \ldots, n$

h_{ij} = duration (h) of diel period i for 24-h period j, $i = 1, \ldots, d_j$, $j = 1, \ldots, n$

$\bar{C}_{ij}$ = average density (no./1000 m^3) for a particular larval fish taxon or for eggs of diel period i for 24-h period j, based on s_{ij} replicate samples

s_{ij} = number of replicate samples of diel period i for 24-h period j

N_j = estimated number of larvae (for a particular taxon) or eggs entrained during 24-h period j

Having calculated the N_j for each 24-h sampling period of the year, the calendar of the sampling year was then divided into sampling blocks. The number of days between any two consecutive 24-h periods of sampling was split evenly between the two periods; the first half of these days was assigned to the sampling block corresponding to the first of

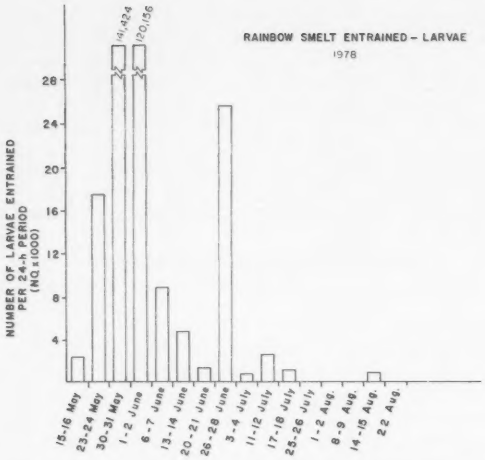

FIG. 1. Total number of rainbow smelt larvae entrained during 24-h sampling periods projected from densities observed in the 16 samples collected weekly at the J. H. Campbell Plant, eastern Lake Michigan, 1978.

these 24-h periods, whereas the second half of these days was included in the sampling block for the second of these 24-h periods. (In the case of an odd number of days between two consecutive 24-h periods, the middle day was split in half.) The first sampling block of the year included the days in the 1st month of sampling prior to the first 24-h sampling period of the year, whereas the last sampling block of the year included the days in the last month of sampling after the last 24-h sampling period of the year. It was assumed that the entrainment rate for every day in any sampling block was the same as for the rate within the 24-h sampling period in that sampling block. The estimate T for the number of larvae (for a particular taxon) or eggs entrained for the entire year is given by the equation:

$$T = \sum_{j=1}^{n} m_j N_j$$

where:

m_j = number of days in sampling block j, $j = 1, \ldots, n$
n = number of 24-h sampling periods for sampling year
N_j = estimated number of larvae (for a particular taxon) or eggs entrained during sampling period j, $j = 1, \ldots, n$
T = estimated total number of larvae (for a certain taxon) or eggs entrained during entire sampling year

Next we calculated the bounds on the error for the number entrained during the 24-h sampling period j, N_j. The upper and lower error bounds for an estimate are equal to the estimate plus or minus, respectively, two times the square root of the variance for the estimate. The variance of N_j is found by the estimator:

$$V(N_j) = f_j^2 \sum_{i=1}^{d_j} (h_{ij})^2 \, V(\bar{C}_{ij})$$

where:

$$V(\bar{C}_{ij}) = \left\{ \left[\sum_{k=1}^{s_{ij}} (C_{ijk} - \bar{C}_{ij})^2 / (s_{ij} - 1) \right] / s_{ij} \right\}$$

$V(\bar{C}_{ij})$ = estimate of the variance of the average density for a particular taxon of diel period i for 24-h period j
C_{ijk} = density observed for a particular taxon for replicate k of diel period i for 24-h period j
$\bar{C}_{ij}$ = average density for a particular taxon of diel period i for 24-h period j
d_j = number of diel periods sampled during 24-h period j
s_{ij} = number of replicate samples of diel period i for 24-h period j
f_j = flow rate for 24-h period j
h_{ij} = duration of diel period i for 24-h period j
N_j = estimated number entrained (for a particular taxon) during 24-h period j
$V(N_j)$ = estimate of variance of N_j

The estimated variance $V(N_j)$ was found based on the assumption that replicate observations were independent of each other within any diel period and between diel periods.

The variance of the estimated number of fish larvae or fish eggs entrained during the entire sampling year can be estimated as:

$$V(T) = \sum_{j=1}^{n} m_j^2 \, V(N_j)$$

where:

m_j = number of days in sampling block j, $j = 1, \ldots, n$
n = number of 24-h sampling periods during year
$V(N_j)$ = estimate of the variance of the estimate of the number entrained for a particular taxon during the 24-h sampling period j
$V(T)$ = estimate of the variance of the estimated total number (for a particular taxon) entrained during the sampling year

This estimation was based on the assumption that the observations were independent between 24-h sampling periods. This was probably not the case for some taxa of fish larvae or for fish eggs where there was a definite pattern in numbers entrained throughout the year.

Variance Adjustment

Loftis and Ward (1979) have derived a method to consider serial correlation in computing variance and have applied it to calculating variances of the annual sample means of several water-quality variables. Each water-quality parameter was observed once a day throughout the sampling year.

The technique developed here to adjust for serial correlation in computing variances is a more general method than the one used by Loftis and Ward, although the basic principle for the adjustment is similar. For entrainment data, we were concerned with autocorrelation among the 24-h sampling periods, that is, autocorrelation within the N_j series. Our method incorporates the lack of homogeneity in the variances

TABLE 1. Estimated numbers of entrained ichthyoplankton with corresponding error bounds for the J. H. Campbell Plant, eastern Lake Michigan, during 1978.

Taxon	Annual entrainment estimate	Two unadjusted standard deviations	Two adjusted standard deviations	% increase in error-bound interval due to adjustment
Alewife	4.89×10^{7}	1.29×10^{7}	1.35×10^{7}	4.8
Yellow perch	1.62×10^{7}	1.83×10^{6}	2.28×10^{6}	24.2
Damaged larvae	3.51×10^{6}	1.32×10^{6}	1.47×10^{6}	11.4
Unidentified Cyprinidae	2.93×10^{6}	4.25×10^{5}	5.08×10^{5}	19.5
Burbot	1.56×10^{6}	4.92×10^{5}	8.19×10^{5}	66.4
Rainbow smelt	1.53×10^{6}	3.04×10^{5}	4.06×10^{5}	33.7
Common carp	1.51×10^{6}	1.94×10^{5}	2.27×10^{5}	17.3
Pomoxis spp.	9.60×10^{5}	1.99×10^{5}	2.69×10^{5}	34.9
Deepwater sculpin (*Myxocephalus thompsoni*)	2.27×10^{5}	1.72×10^{5}	2.02×10^{5}	17.4
Gizzard shad (*Dorosoma cepedianum*)	9.22×10^{4}	9.52×10^{4}	1.14×10^{5}	10.1
Unidentified Catostomidae	6.08×10^{4}	3.35×10^{4}	3.35×10^{4}	0
Lepomis spp.	5.87×10^{4}	5.96×10^{4}	5.96×10^{4}	0
Bluegill (*Lepomis macrochirus*)	4.73×10^{4}	5.17×10^{4}	5.17×10^{4}	0
Goldfish (*Carassius auratus*)	3.58×10^{4}	6.88×10^{4}	6.88×10^{4}	0
Pumpkinseed (*Lepomis gibbosus*)	2.70×10^{4}	5.40×10^{4}	5.40×10^{4}	0
Spottail shiner (*Notropis hudsonius*)	2.58×10^{4}	3.70×10^{4}	3.70×10^{4}	0
Unidentified Coregoninae	2.29×10^{4}	3.68×10^{4}	3.68×10^{4}	0
Ninespine stickleback (*Pungitius pungitius*)	1.65×10^{4}	2.77×10^{4}	2.77×10^{4}	0
White sucker (*Catostomus commersoni*)	1.02×10^{4}	1.06×10^{4}	1.06×10^{4}	0
Emerald shiner (*Notropis atherinoides*)	9.83×10^{3}	2.46×10^{4}	2.46×10^{4}	0
Johnny darter	9.53×10^{3}	2.38×10^{4}	2.38×10^{4}	0
Unidentified pisces	4.90×10^{3}	7.41×10^{3}	7.41×10^{3}	0
Trout-perch (*Percopsis omiscomaycus*)	4.69×10^{3}	7.14×10^{3}	7.14×10^{3}	0
Largemouth bass	1.43×10^{3}	3.33×10^{3}	3.33×10^{3}	0
Fish eggs	1.63×10^{8}	3.59×10^{7}	4.43×10^{7}	23.3

for the N_j terms, whereas in the case of the water-quality series with one observation per sampling period, the variance of the observations was considered constant throughout the year.

Consider the random variables N_t and N_{t+k}, where k is the time lag between the variables. The variance of their sum is:

$$V(N_t + N_{t+k}) = V(N_t) + V(N_{t+k}) + 2\mathrm{Cov}(N_t, N_{t+k}).$$

We used the following estimator for covariance

$$\mathrm{Cov}(N_t, N_{t+k}) = \rho_k \,\mathrm{Var}(N_t)\,\mathrm{Var}(N_{t+k})$$

where ρ_k is the autocorrelation coefficient for lag k. Thus, the variance for the sum T is:

$$V^*(T) = \sum_{i=1}^{n}\sum_{j=1}^{n} m_i\, m_j\, r_{|j-i|}\sqrt{V(N_i)\,V(N_j)}$$

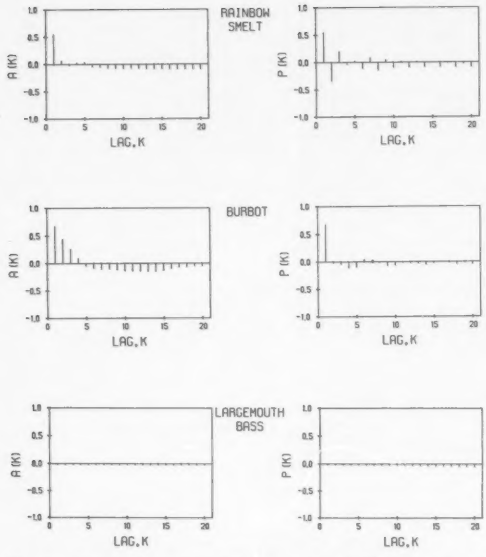

FIG. 2. Estimated autocorrelation functions [$A(K)$] and estimated partial autocorrelation functions [$P(K)$] for rainbow smelt, burbot, and largemouth bass larvae for 24-h sampling period entrainment series at the J. H. Campbell Plant, eastern Lake Michigan, 1978.

where:

m_j = number of days in sampling block j

$r_{|j-i|}$ = estimate of $\rho_{|j-i|}$, the autocorrelation coefficient for lag $|j-i|$, where $|j-i|$ is the absolute value of the quantity $(j-i)$

$V(N_j)$ = estimate of the variance of the estimate of the number entrained for a particular taxon for 24-h sampling period j

n = number of 24-h sampling periods in sampling year

$V^*(T)$ = estimate of the variance for sum T adjusted for non-independence among observations for 24-h periods

The N_j series were identified and then fitted to time series models using techniques described by Box and Jenkins (1976); some of these techniques have been applied to fishery data (Jensen 1976; Madenjian 1979). Bartlett's approximation for the variance of r_k, the estimated autocorrelation coefficient for lag k, was used to check the significance of the estimated autocorrelation function. Based on the time series model chosen, the theoretical autocorrelation for the N_j series was generated and used in calculating the adjusted variance.

Once the variance is found, the upper and lower bounds for the sum T can be found by:

$$T \pm 2\sqrt{V^*(T)}.$$

These are the Chebyshev error bounds for at least 75% confidence; if normality is assumed, these bounds represent 95% confidence limits (Mendenhall et al. 1971).

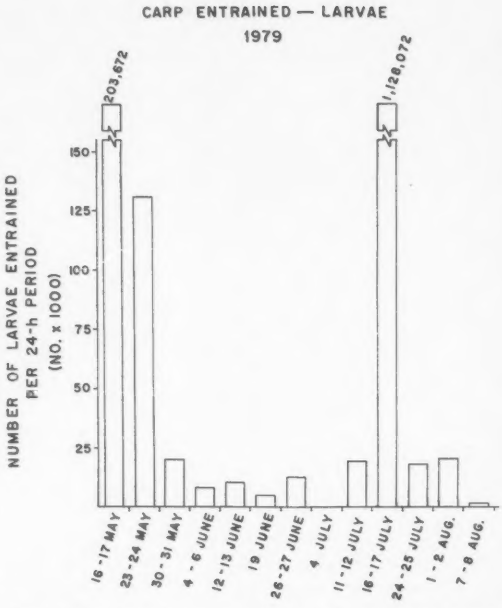

FIG. 3. Total number of common carp larvae entrained during 24-h sampling periods projected from densities observed in the 16 samples collected weekly at the J. H. Campbell Plant, eastern Lake Michigan, 1979.

Results

Of the 54 entrainment series examined for the years 1977 through 1979, 21 (or about 38.9%) showed substantial serial correlation. For the remaining 33 series the observations were considered independent and no variance adjustment was necessary. During 1978 in particular, 9 of the 23 variances were adjusted (Table 1). The adjusted error-bound intervals ranged from 4.8 to 66.4% wider than the corresponding unadjusted intervals for 1978 data, whereas the range was 4.8−87.9% for 1977 through 1979 entrainment data. On the average, for the 21 series with substantial autocorrelation, variance adjustment increased the error-bound interval 26.6%.

Most of the 24-h period entrainment series could be classified into three basic types which can be illustrated by rainbow smelt (*Osmerus mordax*), burbot (*Lota lota*), and largemouth bass (*Micropterus salmoides*) series for 1978. Rainbow smelt showed peak entrainment losses in late May and early June during 1978 (Fig. 1). The estimated autocorrelation and partial autocorrelation functions strongly suggested that an MA(1) model (for moving average process of order 1) was appropriate for the 24-h sampling period entrainment series for this species (Fig. 2). The autocorrelation for the first lag is high, but the remaining autocorrelations are low; the partial autocorrelations decay exponentially and alternate in sign. Estimation of the model parameters and comparisons of the error sum of squares for other applied models supported the MA(1) model as the choice for the smelt

TABLE 2. Estimated numbers of alewife, yellow perch, and rainbow smelt larvae entrained at the J. H. Campbell Plant, eastern Lake Michigan, during 1978. Also included are error bounds for the estimates.

Taxon	Annual entrainment estimate	Two unadjusted standard deviations	Two adjusted standard deviations	% increase in error-bound interval due to adjustment
Alewife prolarvae	2.42×10^{7}	3.29×10^{6}	3.29×10^{6}	0
Alewife postlarvae	2.46×10^{7}	1.23×10^{7}	1.23×10^{7}	0
Yellow perch prolarvae	1.54×10^{7}	2.02×10^{6}	2.44×10^{6}	20.8
Yellow perch postlarvae	7.55×10^{5}	6.21×10^{5}	6.70×10^{5}	7.8
Rainbow smelt prolarvae	1.11×10^{6}	2.69×10^{5}	3.46×10^{5}	28.5
Rainbow smelt postlarvae	3.98×10^{5}	1.44×10^{5}	1.80×10^{5}	24.8

entrainment series in 1978. The width of the adjusted interval for this species was 33.7% greater than the unadjusted one (Table 1). The confidence interval for the adjusted bounds was 1.53 million larvae ± 0.406 million larvae.

The 24-h period entrainment series for burbot larvae in 1978 illustrates an AR(1) process (autoregressive process of order 1). The estimated autocorrelation function decreases exponentially, starting from lag 1, whereas the partial autocorrelation for lag 1 was the only significant partial autocorrelation (Fig. 2). Adjustment increased the bound interval by 66.4% (Table 1).

A "white noise" series, i.e. a series where observations among 24-h sampling periods were independent of each other, is illustrated by the 24-h period entrainment series for largemouth bass for 1978. All autocorrelations and partial autocorrelations were insignificant; thus, no adjustment of the error bounds was necessary (Fig. 2, Table 1). Largemouth bass larvae were collected during only one 24-h period in 1978.

There were a few cases, such as common carp (*Cyprinus carpio*) larvae in 1979, in which a taxon of larvae was frequently entrained but for which serial correlation was not important in the N_j series. The 1979 carp series showed a pronounced spike in July (Fig. 3); spike refers to a single observation substantially greater (approximately an order of magnitude or more) than nearby observations in the series. None of the autocorrelations or partial correlations was significant and variance adjustment was negligible.

The fish egg series for 1978 was identified as an AR(1) process and the variance was adjusted accordingly (Table 1). Most fish eggs entrained were believed to be those of alewife (*Alosa pseudoharengus*).

Variance estimation for the annual entrainment total for stages of alewife, yellow perch (*Perca flavescens*), and rainbow smelt larvae were performed. Prolarvae were defined as larvae in the stage from time of hatching to complete absorption of the yolk sac, whereas postlarvae were larvae in the stage after yolk absorption but before or at a length of 25.4 mm. Results showed that for prolarvae and postlarvae of yellow perch and rainbow smelt in 1978, the time series structures for the 24-h entrainment series were similar to the structure for the respective parent series in which the two stages were pooled; however, the magnitude of the first autocorrelation was somewhat less for the series by larval fish stage than the respective pooled series. Consequently the adjusted error bound was a higher percentage of the corresponding unadjusted interval for the parent series than for the stage series (Tables 1 and 2). However, the stage separation for alewife in 1978 led to two series in which autocorrelations were relatively weak and were determined to be "white noise" series. Note that splitting the alewife pooled series resulted in two series with pronounced spikes similar to the one calculated for the 1979 carp series.

The postlarvae series for alewife in 1979 showed a relatively strong first lag autocorrelation, whereas this autocorrelation for the corresponding prolarvae series was weak. Thus the postlarvae series required a substantial adjustment to its variance (an increase of 60.8% in the error-bound interval), although the prolarvae series required no adjustment at all. The prolarvae series exhibited a spike in July 1979.

Discussion

Serial correlation in the entrainment data did not appear to be more important for one stage of larvae than another. The presence of spikes in the 24-h entrainment series for the more common taxa of fish larvae and for fish eggs seemed most important in determining the impact of serial correlation on the variance of the annual entrainment total. Spikes in the series were associated with reduced autocorrelations and less importance of serial correlation compared with relatively spikeless series. The 24-h entrainment series exhibiting the highest degree of serial correlation were from those taxa which were represented continuously in entrainment samples for a period of at least 10–12 wk, during which time no spikes were present. In general, serial correlation could be ignored in calculating variance of annual entrainment for taxa of larvae or eggs entrained infrequently, such as those taxa represented in entrainment samples fewer than 6 wk of the year.

Of the entrainment series where non-independence of observations should be considered, AR(1) or MA(1) models seemed adequate to model the series. Similarly, Loftis and Ward (1979) used AR(1), AR(2), and ARMA(1, 1) models for water-quality time series. The first-time lag was the most important in modeling the series. Indeed, the magnitude of the first autocorrelation could be considered an index to the importance of the serial correlation factor in the series.

We suspect, as Loftis and Ward (1980) found for water-quality data, that the magnitude of the contribution of non-independence to the variance of annual entrainment depends on the frequency of entrainment sampling. We have shown autocorrelation in the entrainment series to be important in some cases for once-a-week sampling and expect it to be even more important with more frequent sampling. Conversely the effect of serial correlation should decrease as sampling frequency decreases so that for a sampling frequency of once every 2 wk, non-independence of observations probably plays a much less significant role in the variance of the annual entrainment estimate than for once-a-week sampling.

It has been shown that the assumption of independence of entrainment observations could result in substantial underestimation of the variance of the annual entrainment estimate, particularly in the case of common species with relatively spikeless entrainment series. Any decisions based on these underestimated intervals might be in error. For example, the annual entrainment estimate for 1 yr may appear to be significantly greater than that for another year when actually it is not. The procedures illustrated above could be used for calculating number of larvae and eggs entrained with the appropriate error bounds for any power plant with similar sampling design, but are not limited in application to entrainment data. They may be applied to any series provided the series is based on relatively frequent and regular observations.

One application of this variance adjustment procedure is to fish impingement data. Impingement samples have been collected regularly at a number of power plants; samples are collected once every 4 d at many of these plants. Some extensive records of impingement, such as records for every day of 1975 at the D. C. Cook Nuclear Plant on Lake Michigan at Bridgman, Michigan, are available so that impingement series could be modeled as time series with a high degree of accuracy. Preliminary examination of the autocorrelations and partial autocorrelations for the 1975 impingement series for the Cook Plant indicate that for several species, such as alewife, johnny darter (*Etheostoma nigrum*), and slimy sculpin (*Cottus cognatus*), serial correlation should be accounted for in the variance of the annual impingement total.

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Box, G. E. P., and G. M. Jenkins. 1976. Time series analysis: forecasting and control. Holden-Day, San Francisco, CA. 533 p.

Jensen, A. L. 1976. Time series analysis and forecasting of Atlantic menhaden catch. Chesapeake Sci. 17: 305–307.

Jude, D. J. 1975. Entrainment of fish larvae and eggs on the Great Lakes, with special reference to the D. C. Cook Nuclear Plant, southeastern Lake Michigan, p. 177–199. *In* L. D. Jensen [ed.] Proceedings of the Third National Workshop on Entrainment and Impingement. Ecological Analysts, Inc., Melville, New York. 425 p.

Jude, D. J., G. R. Heufelder, N. A. Auer, H. T. Tin, S. A. Klinger, P. J. Schneeberger, C. P. Madenjian, T. L. Rutecki, and G. G. Godun. 1980. Adult, juvenile and larval fish populations in the vicinity of the J. H. Campbell Power Plant, eastern Lake Michigan, 1979. Spec. Rep. No. 79, Great Lakes Res. Div., Univ. Mich., Ann Arbor, MI. 607 p.

Loftis, J. C., and R. C. Ward. 1979. Regulatory water quality monitoring networks — statistical and economic considerations. U.S. Environmental Protection Agency Report No. EPA-600/4-79-055.

1980. Water quality monitoring — some practical sampling frequency considerations. Environ. Manage. 4: 521–526.

Madenjian, C. P. 1979. Time series analysis and forecasting of fishery catch and effort. M.S. thesis, Univ. Mich., Ann Arbor, MI. 54 p.

Mendenhall, W., L. Ott, and R. L. Schaeffer. 1971. Elementary survey sampling. Duxbury Press, Belmont, CA. 247 p.

Snyder, D. E. 1975. Passage of fish eggs and young through a pumped storage generating station. J. Fish. Res. Board Can. 32: 1259–1266.

Teleki, G. C. 1976. The incidence and effect of once-through cooling on young-of-the-year fishes at Long Point Bay, Lake Erie: a preliminary assessment, p. 387–393. *In* G. W. Esh and R. W. McFarlane [ed.] Thermal ecology II. Energy Resource Development Admin., Tech. Info. Center, U.S. Dep. Comm., Springfield, VA. 404 p.

Survival, Respiration, and Food Assimilation of *Daphnia magna* Exposed to Petroleum- and Coal-Derived Oils at Three Temperatures[1,2]

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ULLRICH, S. O. JR., AND R. E. MILLEMANN. 1983. Survival, respiration, and food assimilation of *Daphnia magna* exposed to petroleum- and coal-derived oils at three temperatures. Can. J. Fish. Aquat. Sci. 40: 17–26.

Acute toxicity tests with the water-soluble fractions (WSFs) of both oils showed that mortality of *Daphnia magna* was directly related to temperature and the WSF concentration. The coal-derived oil was more toxic than the diesel fuel oil. The 48-h LC50s for the former were 0.70, 0.44, and 0.18% at 10, 20, and 25°C, respectively; the values for the diesel oil WSF were 87, 32, and 9.7% at 10, 20, and 25°C, respectively. Respiration rates of animals exposed to sublethal concentrations of the WSFs at 10, 20, and 25°C were significantly affected by the WSF concentration of the oils and temperature. The interaction between the concentration of each oil with temperature was statistically significant. Low concentrations of diesel oil WSF stimulated respiration rates at each temperature, but higher concentrations depressed them. At all temperatures, oxygen consumption rates of animals exposed to the coal-derived oil WSF decreased with increased concentration. The exposure to sublethal concentrations of both oils affected food assimilation of the animals in a manner similar to that observed when respiration was the criterion of toxic effect. The interaction between diesel oil WSF concentrations and temperature, but not between coal oil WSF concentrations and temperature, was statistically significant. At 20 and 25°C, low concentrations of diesel oil WSF stimulated assimilation rates, whereas low concentrations of the coal oil WSF depressed them. Generally, high concentrations of both WSFs depressed assimilation rates below control values. These results emphasize the importance of natural stresses, such as temperature, in enhancing toxicity of synthetic chemicals to aquatic organisms, and they reinforce the need to consider such variables as season of the year in evaluating biotic effects of oil spills.

Key words: temperature, *Daphnia magna*, petroleum, coal oil, synthetic oil, respiration, food assimilation, acute toxicity, chronic toxicity

ULLRICH, S. O. JR., AND R. E. MILLEMANN. 1983. Survival, respiration, and food assimilation of *Daphnia magna* exposed to petroleum- and coal-derived oils at three temperatures. Can. J. Fish. Aquat. Sci. 40: 17–26.

Des analyses de la toxicité aiguë des fractions hydrosolubles (FH) des deux huiles révèlent que la mortalité de *Daphnia magna* est directement reliée à la température et à la concentration des FH. L'huile de goudron de houille, dont la CL-50 après 48 h est 0,70, 0,44 et 0,18 % à 10, 20 et 25°C respectivement, est plus toxique que l'huile diesel, avec des valeurs de 87, 32 et 9,7 % à 10, 20 et 25°C respectivement. Les taux de respiration des animaux exposés à des concentrations sublétales de FH à 10, 20 et 25°C sont modifiés de façon significative par la concentration des FH des huiles et la température. L'interaction entre la concentration de chaque huile et la température est statistiquement significative. De basses concentrations de FH d'huile diesel stimulent les taux de respiration à toutes les températures, mais de plus hautes concentrations les réduisent. À toutes les températures, les taux de consommation d'oxygène des animaux exposés aux FH d'huile de goudron de houille diminuent avec une augmentation de la concentration. L'exposition à des concentrations sublétales des deux huiles influe sur l'assimilation de la nourriture de manière semblable à celle observée

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quand la respiration sert de critère d'incidence toxique. L'interaction entre les concentrations de FH d'huile diésel et la température, mais non entre les concentrations de FH d'huile de goudron de houille et la température, est statistiquement significative. À 20 et 25°C, de basses concentrations de FH d'huile diesel stimulent les taux d'assimilation, tandis que de basses concentrations de FH d'huile de goudron de houille les abaissent. En général, des concentrations élevées de FH des deux huiles réduisent les taux d'assimilation à des valeurs inférieures à celles du contrôle. Ces résultats soulignent l'importance des stress naturels, dont la température, dans l'accroissement de la toxicité des produits chimiques synthétiques pour les organismes aquatiques et accentuent le besoin de considérer les variables, dont la saison, au cours de l'évaluation des effets biotiques des déversements de pétrole.

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DWINDLING petroleum reserves, environmental concerns with combustion of fossil fuels, and expansive coal reserves have provided the impetus for the development of coal-conversion processes. Of these processes coal liquefaction will produce fuels that are intended to replace petroleum-derived products (Gehrs 1977). More than 37.8×10^6 L (10^7 gal) of petroleum have been spilled annually into U.S. waters, with pipelines, onshore facilities, and ships accounting for most of the volume (Jones et al. 1977). Pipelines will probably not be used to transport synthetic oils, but barges, railroad cars, and storage facilities will be potential sources for leakage of such oils into aquatic environments.

Most of the research on the toxicity of petroleum to aquatic organisms has been with marine species probably because of the predominance of ocean spills over those in freshwater, although 60% of the annual small (<378 500 L or 100 000 gal) spills have been into freshwater systems (U.S. EPA 1977). Moreover, little research has involved coal-derived oils, which are different chemically from petroleum (Guerin et al. 1981). Thus, extrapolation of toxicity data for petroleum to coal-derived oils is not valid (Giddings et al. 1980; States et al. 1980; Giddings and Washington 1981). In addition to man-induced stresses (e.g. from oil spills), aquatic organisms encounter natural stresses such as temperature changes. Because animals are exposed to seasonal changes in temperature, it is important to understand how these temperature fluctuations will affect the organisms' ability to survive in the presence of spilled oil. There have been no studies to our knowledge on the interaction between these stresses with freshwater species. Thus, we determined the effects of interactions between temperature and the water-soluble fractions (WSFs) of a coal-derived crude oil and a petroleum-derived oil on the survival, respiration, and food assimilation of *Daphnia magna*. WSFs were used instead of whole oils because most of the toxicity of an oil is from its water-soluble components (Evans and Rice 1974; Moore and Dwyer 1974; Rice et al. 1977). Also, spilled oil can be contained and recovered, but the water it contacts will affect a larger area and for a longer time.

Materials and Methods

ACUTE TOXICITY

Daphnia magna came from a stock obtained from Miami University, OH, in 1977. Individual adult females, which were replaced monthly from stock cultures, were maintained in 50 mL of unfiltered well water. Water was changed on alternate days and at those times 1 mL of trout chow suspension was added and the organisms checked for viability. The adult females were acclimated to one of the three test temperatures for at least 2 wk before collection of their offspring, so the young used in the experiments had developed at the appropriate test temperature.

Test materials were a No. 2 diesel fuel oil and a crude oil from the H-Coal direct liquefaction process. The former was purchased locally, and the synthetic oil was obtained from the H-Coal Process Development Unit in Lawrenceville, NJ. The latter oil, which is not necessarily representative of the final commercial product, was from the unit's run 9 (syncrude mode) in September 1979 with Kentucky No. 11 as the feedstock coal. It was a 1.8:1 blend of atmospheric separator overhead and atmospheric separator bottoms. Both oils were stored at 4°C in amber bottles before use.

The WSFs were prepared by layering 1 part oil on 8 parts of filtered well water (pH 7.34, dissolved oxygen 9.3 ± 0.51 mg/L, total alkalinity 150 mg/L as $CaCO_3$, hardness 134 ± 18.0 mg/L as $CaCO_3$). The mixture was stirred gently in a sealed glass bottle for 16 h at 25°C. The suspension was then separated and the WSF filtered through Whatman No. 42 paper. Test concentrations, which were prepared by dilution of the stock WSF with filtered well water, were equilibrated in covered beakers to the desired temperature in environmental chambers for at least 4 h. After equilibration, the WSFs were analyzed for total organic carbon (TOC). To reduce loss of volatile organic compounds, they were not purged during TOC analysis. A well-water blank was similarly analyzed and the amounts present were subtracted from the WSF values (Giddings et al. 1980).

Groups of 10 animals (less than 48 h old) were exposed to 80 mL of the test solution in covered 100-mL beakers. The beakers were placed in environmental chambers at 10, 20, or 25°C under a 12-h light and 12-h dark photoperiod. Illumination from cool-white fluorescent bulbs ranged from 800 to 1600 lx. Three replicates were used for each concentration and also for the well-water control. During the tests, solutions were not renewed or aerated and the animals were not fed. Dissolved oxygen levels did not fall below 6 mg/L and the pH ranged from 7.0 to 8.0 during the tests. Organisms caught in the surface film were resubmerged with a drop of test

solution. Death was defined as the absence of appendage and body movement after gentle swirling of the test solution (Goss 1978). The animals were checked periodically for behavioral changes, mortality, and molting as shown by the presence of cast carapaces. At those times, dead animals and cast exoskeletons were removed from the beakers.

The 48-h lethal concentrations (LC50s) of the toxicants at each temperature were estimated using probit analysis (Finney 1971). Analyses were done on the $\log_{10}$ transformation of the concentrations (APHA 1975; Stephan 1975). Corrections were made for excessive mortality according to the method of Tattersfield and Morris (1924).

Respiration

Oxygen consumption of immature *D. magna* acclimated to 10, 20, or 25°C from birth was measured during their exposure to sublethal concentrations of the WSFs of coal-derived crude oil and No. 2 diesel fuel oil. The test concentrations used (see Ullrich 1981) were those that killed 5, 10, 20, 30, and 50% of the animals in our 48-h acute toxicity tests. Results of these tests indicated that a fixed mortality rate approach as described by McGinniss (1978) is more suitable than one using fractions of the LC50 value for evaluating the interactive effect of temperature and sublethal concentrations of oil on the respiration of *D. magna*. This approach incorporates the slope of the dose–response curve when predicting sublethal levels of comparable effect.

The animals were fed before the tests to minimize the effects of starvation on oxygen consumption (Tatem 1977). At the start of the test, animals (1.10 ± 0.2 mm in length) were placed in 30-mL glass-stoppered flasks containing 30 mL of test solution. The flasks, each with 20 animals, were sealed, checked for air bubbles, and placed in an environmental chamber at one of the three test temperatures (10, 20, or 25°C). Three replicates and two toxicant controls without animals were used for each of the five test concentrations at each temperature. There were also five well-water controls at each temperature, three with and two without animals. During the tests, periodic observations were made on animal behavior and survival. All tests were done at the same time of day to minimize differences in oxygen consumption related to diurnal fluctuations (Duval and Green 1976).

After 8 h the tests were ended, and at that time the dissolved oxygen (DO) concentrations were determined using Burke's (1962) method, except a 1.0-mL sample was used instead of 10 mL for titration with 0.025 mol sodium thiosulfate/L. Oxygen consumption by *D. magna* was calculated as the difference between DO concentrations of the experimental flasks and those of the toxicant controls. The rates are expressed as $\mu L\ O_2 \cdot mg\ dry\ wt^{-1} \cdot h^{-1}$.

Food Assimilation

Assimilation rates of the alga *Chlorella vulgaris* by immature *D. magna*, acclimated to 10, 20, and 25°C, were measured during their exposure to sublethal concentrations of the WSFs of the two oils. These rates were not corrected for carbon loss resulting from respiration. The WSF concentrations were the same as those used in the respiration experiment except the LC5 value which was omitted in the assimilation tests.

Algae were cultured in a modified Bold's medium at 25°C (Nichols and Bold 1965). The cells were harvested during the log phase of growth because senescent cells inhibit *D. magna* feeding rates (Ryther 1954; McMahon and Rigler 1965). They were labeled by exposing them to 0.67 mBq [^{14}C]$NaHCO_3$/L of culture for 12 h. Labeled and unlabeled cells were centrifuged and then counted in a Coulter counter. Algal concentrations were diluted to $1-2 \times 10^6\ \mu m^3/mL$ with the appropriate test oil concentration. Ten 200-mL aliquots of these suspensions were filtered through 0.45-μm Millipore filter paper, dried at 90°C for 48 h, and then weighed. The amount of carbon was assumed to be 48% of the algal cell dry weight (Fogg 1975). These values were converted to mg C/vol and, on the basis of dry cell weight, we used a value of $1.328 \times 10^{-9}\ mg\ C/\mu m^3$ for this study.

Animals, 1.20 ± 0.14 mm in length, were placed in 1-L beakers containing $1-2 \times 10^6\ \mu m^3/mL$ of algal cells for 4 h before tests to minimize fluctuations in assimilation rates (McMahon and Rigler 1965; Schindler 1968). After this 4-h acclimation, animals in groups of 20 were transferred to 100-mL beakers containing 50 mL of the labeled algal suspension. Controls consisted of 50 mL of the algal suspension diluted to a concentration of $1-2 \times 10^6\ \mu m^3/mL$ with filtered well water. Three replicates were used for each WSF concentration and for the controls. Tests were done in an environmental chamber at one of the three test temperatures and under a constant illumination of 800–1600 lx.

After 8 h, animals were transferred to beakers containing 50 mL of unlabeled algal suspension and held for 1.5 h to allow them to eliminate undigested labeled cells (Schindler 1968). At the end of this time, animals that appeared normal were collected on Whatman No. 52 filter paper, rinsed with filtered well water, and then oxidized in a tissue oxidizer. All samples were counted in a liquid scintillation counter for 10 min. Counts were corrected for background, and final activities were determined using the channels ratio method.

Algal radioactivity was determined by filtration of 5-mL aliquots of a known cell concentration through an HA 0.45-μm Millipore filter. Three replicate samples were oxidized, counted, and corrected for background and counting efficiencies. Final activities were expressed as $dpm/\mu m^3$.

Animal lengths and weights were determined from a subsample of 20 from each test group. Measurements were taken from the anterior tip of the helmet to the base of the tail spine (Schindler 1968; Burns 1969). Three samples of 20 animals were dried at 90°C for 48 h and then weighed. Assimilation rates are expressed as $\mu g\ C \cdot mg\ dry\ wt^{-1} \cdot h^{-1}$.

The results from the respiration and food assimilation experiments were analyzed using the Statistical Analysis System (Barr et al. 1976). A two-way factorial analysis of variance was used with the significance level set at $P \leq 0.05$.

Results and Discussion

Survival

The coal-derived oil WSF was more toxic to *D. magna* than the WSF of the petroleum-derived oil. Mortality was

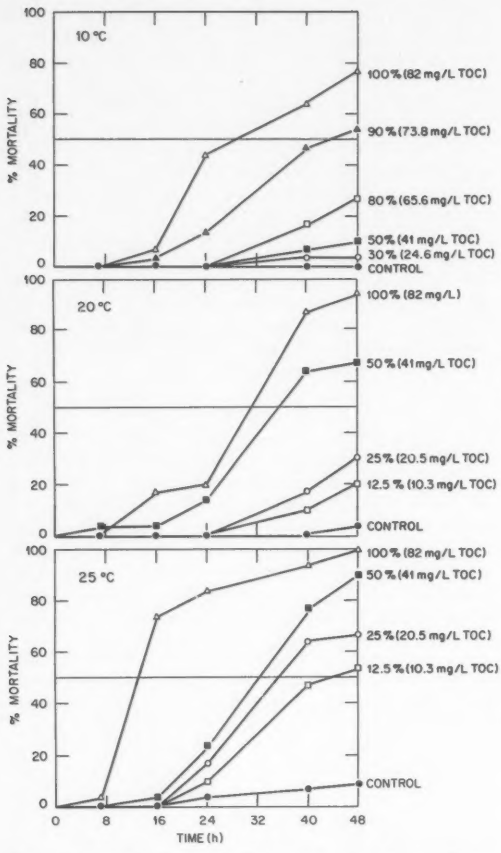

FIG. 1. Mortality rates of *Daphnia magna* exposed to different concentrations of the water-soluble fraction of No. 2 diesel fuel oil at different temperatures. Test duration, 48 h. TOC = total organic carbon.

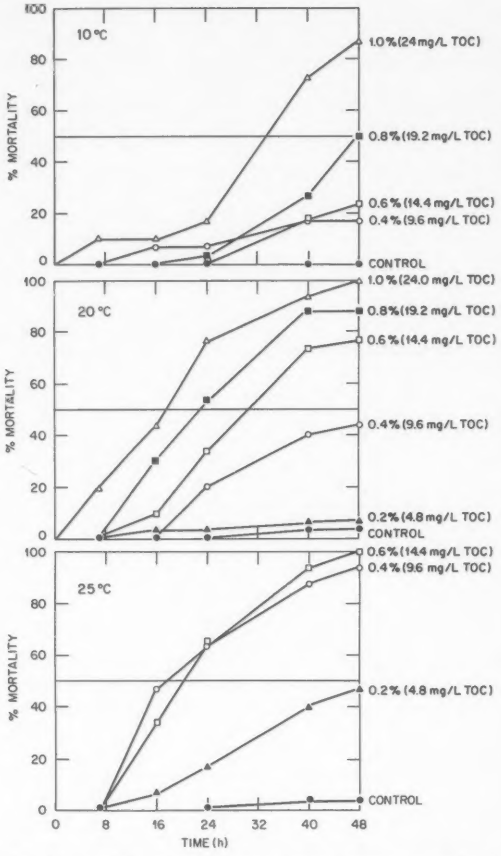

FIG. 2. Mortality rates of *Daphnia magna* exposed to different concentrations of the water-soluble fraction of H-Coal crude oil at different temperatures. Test duration, 48 h. TOC = total organic carbon.

directly related to concentration of the WSF and temperature for both oils (Fig. 1, 2). The 48-h LC50s for the diesel oil WSFs were about two orders of magnitude higher than for the coal-derived WSFs (Table 1). The 48-h LC50 values expressed as TOC also show the greater toxicity of coal-derived oil to *D. magna* (Table 1). Most of the deaths of animals exposed to both oils occurred within the first 40 h of the tests, but time to death was directly dependent on both the concentration of the WSFs and temperature.

More than 50% of the animals exposed to diesel oil WSF molted at all temperatures, and the total number of molts was also temperature dependent. After 6 h, animals at 20 and 25°C were active in all test concentrations, but those at 10°C showed little activity in concentrations above 50%. After 16 h, organisms exposed to diesel oil WSF concentrations below 80% at 10°C were more active than those at higher concentrations. After 24 h, animals at concentrations greater than the LC50 showed little activity. The total number of molts of animals exposed to the coal-derived WSF at 20 and 25°C was higher than that at 10°C, although more than 65% of the animals at 10°C molted during the test. Animals at 20 and 25°C were active after 6 h in all concentrations, but those at 10°C showed little activity in concentrations above 0.6%. Organisms at concentrations greater than the LC50 showed little activity after 24 h at all test temperatures.

This is the first study to our knowledge that shows a direct relationship between temperature and the sensitivity of *D. magna* to WSFs of a coal-derived and a petroleum-derived oil. This relationship, however, has been observed for other pollutants and test organisms. McGinniss (1978) found that *D. pulex*, after acclimation to different temperatures, were more sensitive to simulated refinery and cooling tower blowdown effluents at 20 than at 10°C. Cox (1974) reported that survival of adult mysids (*Mysidopsis almyra*) and brown

shrimp (*Penaeus aztecus*), not acclimated to the test temperatures, was greater after their exposure to crude and refined petroleum products at 21 than at 32°C. Finally, Michael and Brown (1978) found that the survival of the amphipod *Neohaustorius schmitzi*, not acclimated to the test temperatures, was less after exposure to No. 2 diesel fuel oil at 20 than at 10°C.

Mortality rates of our organisms were dependent on the temperature and concentration of the WSF. McGinniss (1978) suggested that the uptake rates of toxins by aquatic organisms are temperature dependent. Thus, our *D. magna* probably absorbed WSF components at a faster rate at the higher temperatures, with the delay in mortality being explained by the time required for the organisms to accumulate toxic levels. Finally, molting rates of *D. magna* and *D. pulex* are directly related to temperature (Goss 1978). Lee and Buikema (1979) suggested that *D. pulex* were most sensitive to toxins during molting when water is absorbed to increase body size. Thus, our results and those of others are consistent with the hypothesis that the direct relationship between temperature and sensitivity of aquatic organisms to toxicants is due to an increase in the toxicant uptake and in molting rates of the organisms with an increase in temperature. Our data, however, are insufficient to confirm this hypothesis.

Our animals exposed to LC50s of the WSFs at 10°C showed little movement during the first 6 h, but they were more active after 16 h. Geiger (1979) reported a similar activity pattern for *D. pulex* exposed to creosote and naphthalene at 20°C. After 24 h, our animals at concentrations greater than the LC50, and at all three temperatures, showed little activity. This finding is not unexpected because Rice et al. (1977) reported that marine organisms exposed to oil also show "narcosis" immediately before death.

We can calculate from our results, using dilution factors as described by States et al. (1980), that the coal-derived WSF was 125 times more toxic than the No. 2 diesel oil WSF to *D. magna* at 10°C, and 75 and 55 times more toxic at 20 and 25°C, respectively. This greater toxicity of a synthetic crude oil compared with a refined petroleum product to *D. magna* is in agreement with results of others. In 48-h tests at 20°C, Giddings et al. (1980) found that the WSF of a coal-derived crude oil was 20 times more toxic to *D. magna* than was No. 2 diesel oil. States et al. (1980) also reported that a coal-derived oil from the Solvent Refined Coal II process was 148 times more toxic to *D. magna* than was No. 6 diesel fuel oil at 20°C.

The toxicity to aquatic organisms of WSFs of petroleum products has been attributed to the high concentrations of aromatic hydrocarbons (Blumer et al. 1970; Moore and Dwyer 1974), especially low boiling point aromatics such as naphthalene (Anderson et al. 1974; Cox 1974; Winters et al. 1976). In contrast, the toxicity of coal-derived oils is linked to the phenolic and nitrogen-containing heterocyclic bases of the WSFs (Giddings et al. 1980; Guerin et al. 1981). We do not know the mechanisms of action of these compounds on *D. magna*. Crisp et al. (1967) reported that low phenol concentrations inhibited locomotion of barnacle nauplii, and Brown et al. (1967) suggested that phenol paralyzes the nervous system and causes cardiovascular congestion in fish. Finally, Guerin et al. (1981) found that coal-derived oils were more mutagenic than petroleum-derived oils in the Ames *Salmonella* test system. The mutagenicity of the former oils is due to their alkaline and neutral fractions, whereas for petroleum, only the neutral fractions are mutagenic. Thus, coal-derived oils may be potentially more hazardous than petroleum-derived products to aquatic organisms. For this reason, they invite concern about their accidental release into aquatic environments and their subsequent effects on the ecosystem.

TABLE 1. Acute toxicity of water-soluble fractions (WSFs) of No. 2 diesel fuel oil and coal-derived oil to *Daphnia magna* at 10, 20, and 25°C.

Temperature, °C	48-h LC50		Slope of probit line[b]
	% WSF	TOC[a]	
	Diesel fuel oil		
10	87.8 (76.1−110.8)[c]	71.9	2.41
20	32.4 (26.1−41.0)	26.6	1.14
25	9.7 (6.73−13.10)	7.95	0.69
	H-Coal oil		
10	0.70 (0.51−0.85)	16.8	2.60
20	0.44 (0.40−0.49)	10.6	2.25
25	0.18 (0.15−0.21)	4.32	1.71

[a]Based on total organic carbon concentrations of 82 and 2400 mg/L in WSFs of No. 2 diesel oil and H-Coal oil, respectively.
[b]Maximum likelihood estimate.
[c]Numbers in parentheses are predicted minimum and maximum LC50s as determined by probit analyses procedure.

RESPIRATION

Respiration rates of *D. magna* were significantly affected by the concentration of diesel oil WSF and temperature ($P < 0.01$). Animals exposed to low concentrations at each test temperature had higher oxygen consumption rates than the controls (Fig. 3). Those exposed to the LC10 at 20°C and to the LC30 at 25°C showed the highest rates compared with their respective controls. Respiration rates of organisms at 10 and 20°C decreased below control values with an increase in the WSF concentration, whereas rates of animals at 25°C were greater than those for controls except for the LC50 (Fig. 3). With increased temperature, the concentration of WSF needed to elicit the respiratory responses decreased.

As with diesel oil, respiration rates of animals exposed to coal-derived oil were significantly affected by the toxicant concentration and by temperature, and there was an interaction between the two variables ($P < 0.01$). Generally, oxygen consumption of animals at all temperatures decreased with increased toxicant concentration (Fig. 4). At all temperatures, the controls and those animals exposed to low WSF concentrations had the highest respiration rates (Fig. 4).

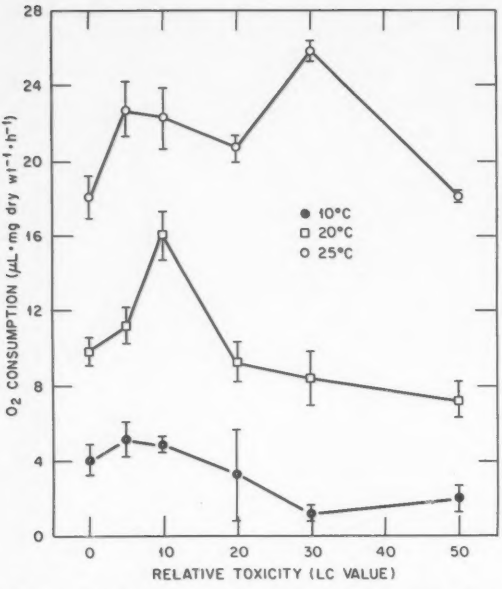

FIG. 3. Effects of an 8-h exposure to sublethal concentrations (expressed as lethal concentration values) of the water-soluble fractions of No. 2 diesel fuel oil and different temperatures on oxygen consumption of *Daphnia magna*. Bars = 2 × SE (N = 3).

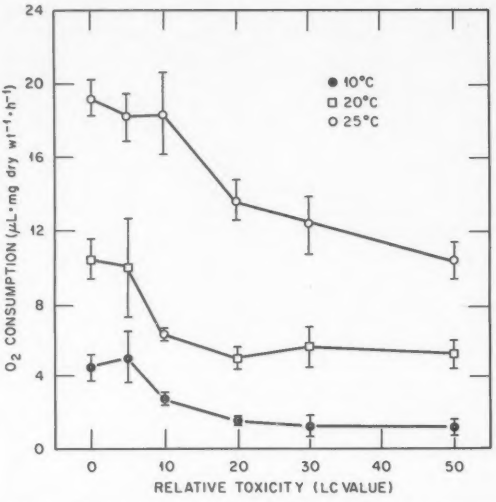

FIG. 4. Effects of an 8-h exposure to sublethal concentrations (expressed as lethal concentration values) of the water-soluble fractions of H-Coal crude oil and different temperatures on oxygen consumption of *Daphnia magna*. Bars = 2 × SE (N = 3).

Animals at 25°C showed the greatest actual reduction in oxygen consumption. As found with animals exposed to diesel fuel, the WSF concentration needed to depress oxygen consumption below that of controls decreased with increased temperature.

Our results show that the oxygen consumption rates of *D. magna* were dependent on the type of oil and the temperature as well as on the interaction between these two stresses. Diesel oil WSF concentrations below the LC10 caused an increase in respiration of organisms at all three temperatures, even though the increase at 10°C was not significant, but at higher concentrations the rates were similar to those organisms exposed to coal-derived oil, i.e. oxygen consumption decreased below control values with increased toxicant concentration. Although those animals exposed to diesel oil at 25°C had rates higher than or similar to the controls at all concentrations, the rate at the LC50 showed a marked decrease compared with rates at lower concentrations. These results suggest that *D. magna* exposed to increased concentrations of diesel oil can eventually reach a tolerance threshold or "response ridge" (Alderdice 1972). At concentrations above this threshold, they are unable to compensate metabolically for the increased stress. A similar response was shown by Laughlin and Neff (1977) for the horseshoe crab *Limulus polyphemus* exposed to petroleum WSF; namely, when WSF concentrations exceeded the threshold tolerance, respiration rates decreased with increased concentration.

The increase in oxygen consumption by our organisms exposed to low concentrations of diesel oil WSF may represent a generalized stress response. Laughlin and Neff (1977) reported a similar respiratory stimulation in *L. polyphemus*. Presumably, with increased toxicant concentrations, specific metabolic systems would become inoperative. Then, as we observed, "narcosis" of the animals would ensue.

The respiration of our animals exposed to low concentrations of coal-derived WSF was not stimulated, as found for *D. magna* with diesel oil WSF, but instead it decreased or remained similar to control rates with increased concentrations. Either the coal-derived oil concentrations we used were not low enough to stimulate respiration, or differences in the composition of the two WSFs could explain the differences in respiratory response. There is evidence to support the latter supposition because WSFs of coal-derived oils contain much higher concentrations of phenol and nitrogen-containing organic bases than does petroleum (Winters et al. 1976; S. E. Herbes, Oak Ridge National Laboratory, personal communication). We do not know the mechanisms of action of these chemicals on *D. magna*, but in fish, phenol paralyzes the nervous system and causes cardiovascular congestion (Brown et al. 1967). Also, Parkhurst et al. (1981) found that acridine, a nitrogen-containing base found in synthetic fuels, partially immobilized *D. magna* at concentrations near the 48-h LC50. Thus, the narcotic action of these compounds could explain the absence of stimulation of respiration in *D. magna* at low concentrations of the coal-derived WSF.

Because many factors can affect metabolism of aquatic organisms, the interactive effect of temperature and the WSFs on oxygen consumption of *D. magna* is difficult to interpret. Animals exposed to either WSFs at 25°C showed respiratory responses that differed more markedly from the controls and through a narrow range of concentrations than did those

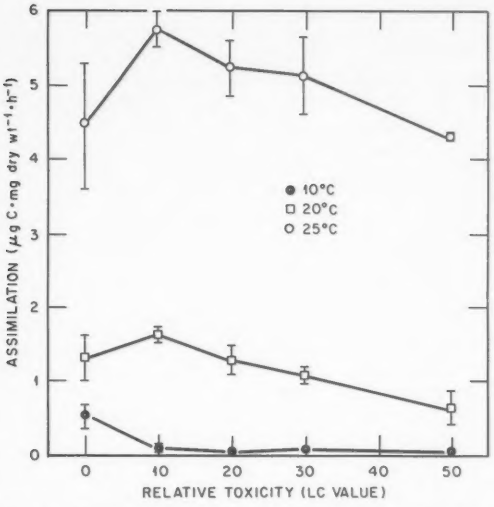

FIG. 5. Effects of an 8-h exposure to sublethal concentrations (expressed as lethal concentration values) of the water-soluble fractions of No. 2 diesel fuel oil and different temperatures on food assimilation of *Daphnia magna*. Bars = 2 × SE (N = 3).

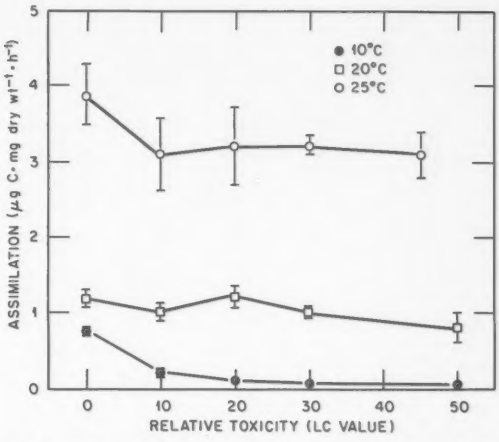

FIG. 6. Effects of an 8-h exposure to sublethal concentrations (expressed as lethal concentration values) of the water-soluble fractions of H-Coal crude oil and different temperatures on food assimilation of *Daphnia magna*. Bars = 2 × SE (N = 3).

organisms at 10 and 20°C. With decreased temperature, the tolerance thresholds of animals exposed to diesel WSF were reached at progressively higher concentrations. Animals exposed to H-Coal WSF showed greater absolute decreases in oxygen consumption with increased temperatures. These findings suggest that temperature enhances the sensitivity of *D. magna* to the toxic action of the WSFs.

Generally, our results showing the effects of interaction between temperature and petroleum on respiration of *D. magna* agree with those previously reported for other species. Laughlin and Neff (1977) found that respiration of *L. polyphemus* was significantly higher than that of control animals exposed to the WSF of No. 2 diesel fuel oil at various combinations of salinity and temperature. Edwards (1978) reported that acute and chronic exposures of the shrimp *Crangon crangon* to the WSFs of a petroleum crude oil at different temperatures affected respiration rates. He found that after acute exposure animals at all temperatures had decreased respiration rates at low WSF concentrations, increased rates at intermediate concentrations, and decreased rates at high concentrations as compared with controls. With chronic exposures, however, organisms at all temperatures had decreased respiration rates with increased WSF concentration.

The effects of petroleum WSFs on the oxygen consumption of our *D. magna* are similar to those found in previous studies. Anderson (1975) reported a similar pattern of respiratory response for mysid shrimp *M. almyra* after a short exposure to No. 2 diesel fuel oil. Lee et al. (1978) found that respiration rates of planktonic shrimp, *Lucifer saxoni*, exposed to No. 2 diesel fuel oil increased at low concentrations and decreased at high concentrations. Finally, Geiger (1979) reported that *D. pulex* that were acclimated to LC20 and LC30 of WSFs of No. 2 diesel fuel oil for two to three molt cycles did not have respiration rates significantly different from controls. In our study, *D. magna* that were not acclimated to LC20 and LC30 of diesel oil also did not have oxygen consumption rates significantly different from the controls. However, animals at the LC10 had significantly higher rates than controls, but those at the LC5 did not. Our results suggest that if Geiger (1979) had exposed his animals to lower concentrations of diesel fuel oil, he also might have found stimulation of respiration rates. Geiger (1979) suggested that the LC20 for petroleum WSFs is a threshold concentration for biological responses. Our results suggest that concentrations lower than the LC20 cause adverse physiological responses and that the actual concentrations necessary to cause these responses are temperature dependent.

FOOD ASSIMILATION

Food assimilation rates of the organisms were significantly affected by the concentration of diesel oil WSF and temperature. A significant interaction was found between temperature and the WSF concentration ($P < 0.01$). Animals exposed to low concentrations at 25°C had rates greater than the controls (Fig. 5). Assimilation rates by organisms at the LC50 at 20°C and those of all animals at 10°C were significantly lower than the controls. The WSF concentrations needed to elicit these response patterns decreased with increased temperature.

The assimilation rates of organisms exposed to coal-derived WSFs were also significantly affected by the WSF concentration ($P < 0.01$) and by temperature ($P < 0.01$), but the interaction between the two variables was not statistically significant. Assimilation rates of animals exposed to H-Coal WSFs decreased below control values with increased concentration at all temperatures except the LC20 at 20°C

(Fig. 6). Of all test animals, those at 25°C had the greatest reduction in assimilation rate as compared with the controls. As found with organisms exposed to diesel oil WSF, the synthetic oil concentrations needed to elicit these changes decreased with increased temperature.

This is the first study to our knowledge on the effects of the interaction between temperature and WSF of oils on food assimilation rates of aquatic organisms. Previous studies, which include those of Gilfillan (1975) with mussels (*Mytilus edulis* and *Modiolus demissus*), Wells and Sprague (1976) with lobsters (*Homarus americanus*), Keck et al. (1978) with clams (*Mercenaria mercenaria*), and Berman and Heinle (1980) with copepods (*Acartia clausi* and *A. tonsa*), dealt with the effects of petroleum on feeding or assimilation of marine organisms. Our results agree with theirs except they did not report stimulation of assimilation rates by low petroleum concentrations.

The effects of the WSFs on food assimilation were similar to those we found when respiration was the criterion of toxic effect; namely, for diesel oil WSF there was a stimulation of rates by low concentrations, except at 10°C, but a depression at high concentrations. In contrast, there was a depression of rates at all concentrations of the coal-derived oil WSF. The relationship between the magnitude of these responses and temperature was similar to that which we found in the respiration studies. Animals at low concentrations of WSFs at 25°C had higher assimilation rates, as compared with controls, that did those at 10 and 20°C. Also, animals exposed to the coal-derived oil at 25°C had greater decreases in assimilation rates, as compared with controls, than did those animals at 10 and 20°C.

Geiger and Buikema (1981) studied the filtration, but not the assimilation, rates of *D. pulex* exposed to WSFs of No. 2 diesel fuel oil at 20°C. Their animals, which were acclimated to the LC20 and LC30 for several molt cycles, had rates significantly higher than the controls, with those at the LC20 having rates higher than those at the LC30. In contrast, our *D. magna* exposed to the LC20 and LC30 of No. 2 diesel fuel oil WSF at 20°C had assimilation rates slightly, but not significantly, lower than controls. A result common to both studies was shown by animals at the LC20's which had filtration and assimilation rates higher than those of animals at the LC30's. Geiger (1979) suggested that the LC20 for petroleum WSFs is the threshold for biological responses by *Daphnia* spp. Our results show that *D. magna* can be sensitive to concentrations of petroleum and coal-derived WSFs as low as the LC10.

We did not correct for respiratory carbon loss by the animals during the tests. Lampert (1977) showed that significant quantities of labeled carbon were respired by *D. pulex* during a 3-h exposure to labeled algae. The amount depended on the temperature, food concentration, and the size of the animal. He states that such losses would result in underestimation of assimilation rates. Schindler (1968) and Kibby (1971), however, showed that *Daphnia* spp. respired negligible amounts of labeled carbon for 16 h after a 6-h exposure to labeled algae. On the basis of their results, considering the variability in the respiratory responses of our animals to both WSFs, and because of our short exposure times, we decided that corrections for carbon loss would not yield meaningful additional information. With such corrections, our control animals would probably have shown higher assimilation rates.

In summary, the interactions between temperature and sublethal oil concentrations on respiration and assimilation of *D. magna* are similar to those shown in our acute toxicity tests; i.e. in the acute tests, deaths of animals exposed to the oil WSFs were directly related to temperature. Animals at the highest temperature not only had the higher mortality rates but for a given concentration the deaths occurred sooner than did those of organisms at the lower temperatures. For assimilation and respiration, organisms at the highest temperature showed greater absolute changes, as compared with their respective controls, than did those at the two lower temperatures. In addition, changes in assimilation and respiration occurred at lower toxicant concentrations than they did for animals at the lower temperatures. These results emphasize the importance of natural stresses, such as temperature, in enhancing toxicity of synthetic chemicals to aquatic organisms; more specifically, they reinforce the need to consider such variables as season of the year in evaluating the hazards of oil spills to aquatic biota. Finally, our results add further evidence for the greater toxicity of coal-derived oils as compared with petroleum to aquatic organisms.

Acknowledgments

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ALDERICE, D. F. 1972. Responses of marine poikilotherms to environmental factors acting in concert, p. 1659–1722. *In* E. D. Kinne [ed.] Marine Ecology. Wiley-Interscience, New York, NY.

AMERICAN PUBLIC HEALTH ASSOCIATION (APHA). 1975. Standard methods for examination of water and wastewater. 14th ed. Washington, DC. 1193 p.

ANDERSON, J. W. 1975. Laboratory studies on the effects of oil on marine organisms: an overview. Publication No. 4249, American Petroleum Institute, Washington, DC.

ANDERSON, J. W., J. M. NEFF, B. A. COX, H. E. TATEM, AND G. M. HIGHTOWER. 1974. Characteristics of dispersions and water-soluble extracts of crude and refined oils and their toxicity to estuarine crustaceans and fish. Mar. Biol. 27: 75–88.

BARR, A. J., J. H. GOODNIGHT, J. P. SALL, AND J. T. HELWIG. 1976. A user's guide to SAS76. SAS Institute Inc., Raleigh, NC. 329 p.

BERMAN, M. S., AND D. R. HEINLE. 1980. Modification of feeding behavior of marine copepods by sublethal concentrations of water-accommodated fuel oil. Mar. Biol. 56: 59–64.

BLUMER, M., S. SOUZA, AND J. SASS. 1970. Hydrocarbon pollution of edible fish by an oil spill. Mar. Biol. 5: 195–202.

BROWN, V. M., D. H. M. JORDAN, AND B. A. TILLER. 1967. The effect of temperature on the acute toxicity of phenol to rainbow trout in hard water. Water Res. 1: 587–594.

BURKE, J. D. 1962. Determination of oxygen in water using a 10 mL syringe. J. Elisha Mitchell Sci. Soc. 78: 145–147.

BURNS, C. W. 1969. Relation between filtering rate, temperature, and body size in four species of *Daphnia*. Limnol. Oceanogr. 14: 693–700.

COX, B. A. 1974. Responses of the marine crustacean, *Mysidopsis almyra* Bowman, *Penaeus aztecus* Ives, and *Penaeus setiferus*

(Linn.) to petroleum hydrocarbons. Ph.D. thesis, Texas A&M University, College Station, TX. 167 p.

CRISP, D. J., A. O. CHRISTIE, AND A. F. A. GHOBASHY. 1967. Narcotic and toxic action of organic compounds on barnacle larvae. Comp. Biochem. Physiol. 22: 629–649.

DUVAL, W. S., AND G. H. GREEN. 1976. Diel feeding and respiration rhythms in zooplankton. Limnol. Oceanogr. 21: 823–829.

EDWARDS, R. R. C. 1978. Effects of water-soluble oil fractions on metabolism, growth, and carbon budget of the shrimp *Crangon crangon*. Mar. Biol. 46: 259–265.

EVANS, D. R., AND S. D. RICE. 1974. Effects of oil on marine ecosystems: a review for administration and policy makers. Fish. Bull. 72: 625–838.

FINNEY, D. J. 1971. Probit analyses. Cambridge University Press, London. 222 p.

FOGG, G. W. 1975. Algal cultures and phytoplankton ecology. 2nd ed. Univ. Wisconsin Press, Madison, WI. 175 p.

GEHRS, C. W. 1977. Environmental implications of coal conversion technologies: organic contaminants, p. 157–175. *In* J. H. Thorp and J. W. Gibbons [ed.] 1977 Symposium on Energy and Environmental Stress in Aquatic Systems. CONF-77114. Technical Information Center, Oak Ridge, TN.

GEIGER, J. G. 1979. The effects of water-soluble fractions of naphthalene, phenanthrene, No. 2 fuel oil, coal tar creosote on the freshwater cladoceran, *Daphnia pulex*. Ph.D. thesis, Virginia Polytechnic Institute and State University. Blacksburg, VA. 108 p.

GEIGER, J. G., AND A. L. BUIKEMA JR. 1981. Oxygen consumption and filtering rate of *Daphnia pulex* after exposure to water-soluble fractions of naphthalene, phenanthrene, No. 2 fuel oil, and coal-tar creosote. Bull. Environ. Contam. Toxicol. 27: 783–789.

GIDDINGS, J. M., B. R. PARKHURST, C. W. GEHRS, AND R. E. MILLEMANN. 1980. Toxicity of a coal liquefaction product to aquatic organisms. Bull. Environ. Contam. Toxicol. 25: 1–6.

GIDDINGS, J. M., AND J. N. WASHINGTON. 1981. Coal-liquefaction products, shale oil, and petroleum. Acute toxicity to freshwater algae. Environ. Sci. Technol. 15: 106–108.

GILFILLAN, E. S. 1975. Decrease of net carbon flux in two species of mussels caused by extracts of crude oil. Mar. Biol. 29: 53–57.

GOSS, L. B. 1978. The effect of temperature on *Daphnia pulex* Leydig and *Daphnia magna* Straus. Ph.D. thesis, University of Tennessee, Knoxville, TN. 123 p.

GUERIN, M. R., I. B. RUBIN, T. K. RAO, B. R. CLARK, AND J. L. EPLER. 1981. Distribution of mutagenic activity in petroleum and petroleum substitutes. Fuel 60: 282–288.

JONES, D. C., W. S. CLARK, W. F. HOLLAND, J. C. LACY, AND E. D. SETHNESS. 1977. Monitoring environmental impacts of the coal and oil shale industries: research and development needs. EPA-60017-77-015 U.S. Environ. Prot. Agency, Las Vegas, NV. 193 p.

KECK, R. T., R. C. HESS, J. WEHMILLER, AND D. MAUER. 1978. Sublethal effects of the water-soluble fractions of Nigerian crude oil on the juvenile hard clams, *Mercenaria mercenaria*. Environ. Pollut. 15: 109–119.

KIBBY, H. V. 1971. Energetics and population dynamics of *Diaptomus gracilis*. Ecol. Monogr. 41: 311–327.

LAMPERT, W. 1977. Studies on the carbon balance of *Daphnia pulex* DeGeer as related to environmental conditions. I. Methodological problems of the use of ^{14}C for the measurement of carbon assimilation. Arch. Hydrobiol. 48: 287–309.

LAUGHLIN, R. B. JR., AND J. M. NEFF. 1977. Interactive effects of temperature, salinity, shock and chronic exposure to No. 2 fuel oil on survival, development rate, and respiration of the horseshoe crab *Limulus polyphemus*, p. 182–191. *In* D. A. Wolfe [ed.] Fate and effect of petroleum hydrocarbons in marine ecosystems and organisms. Pergamon Press, New York, NY. 78 p.

LEE, D. R., AND A. L. BUIKEMA JR. 1979. Molt-related sensitivity of *Daphnia pulex* in toxicity testing. J. Fish. Res. Board Can. 36: 1129–1133.

LEE, W. Y., K. WINTERS, AND J. A. C. NICOL. 1978. The biological effects of the water-soluble fractions of No. 2 fuel oil on the planktonic shrimp *Lucifer faxoni*. Environ. Pollut. (Ser. A) 15: 167–183.

MCGINNISS, J. M. 1978. The effect of temperature on the sensitivity of *Daphnia pulex* to two simulated industrial effluents. M.S. thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA. 89 p.

MCMAHON, J. W., AND F. H. RIGLER. 1965. Feeding rate of *Daphnia magna* Straus in different foods labeled with radioactive phosphorus. Limnol. Oceanogr. 10: 105–114.

MICHAEL, A. D., AND B. BROWN. 1978. Effects of laboratory procedure on fuel oil toxicity. Environ. Pollut. 15: 277–287.

MOORE, S. F., AND R. L. DWYER. 1974. Effects of oil on marine organisms: a critical assessment of published data. Water Res. 8: 819–827.

NICHOLS, H. W., AND H. C. BOLD. 1965. *Trichosarcina polymorpha* gen. et sp. nov. J. Phycol. 1: 34–38.

PARKHURST, B. R., A. S. BRADSHAW, J. L. FORTE, AND G. P. WRIGHT. 1981. The chronic toxicity to *Daphnia magna* of acridine, a representative azaarene present in synthetic fossil-fuel products and wastewaters. Environ. Pollut. (Ser. A) 24: 21–30.

RICE, S. D., J. W. SHORT, AND J. F. KARINEN. 1977. Comparative oil toxicity and comparative animal sensitivity, p. 78–94. *In* D. A. Wolfe [ed.] Fate and effects of petroleum hydrocarbons in marine ecosystems and organisms. Pergamon Press, New York, NY. 78 p.

RYTHER, J. W. 1954. Inhibitory effects of phytoplankton upon feeding of *Daphnia magna* with reference to growth, reproduction, and survival. Ecology 35: 522–533.

SCHINDLER, D. W. 1968. Feeding assimilation, and respiration rates of *Daphnia magna* under various environmental conditions and their relations to production estimates. J. Anim. Ecol. 37: 369–385.

STATES, J. B., S. A. BARRACLOUGH, D. D. DAUBLE, W. E. FALLON, J. R. SKALSKI, R. M. BEAN, AND R. H. GRAY. 1980. Comparative toxicity of a coal liquid and three reference oils to a freshwater invertebrate, *Daphnia magna*, (Abst.). *In* Coal conversion and the environment: chemical, biomedical, and ecological considerations. 20th Hanford Life Sciences Symposium, Battelle Memorial Institute, Richland, WA.

STEPHAN, C. E. 1975. Methods for acute toxicity tests with fish, macroinvertebrates, and amphibians. EPA-660/3-75-009. U.S. Environ. Prot. Agency, Corvallis, OR.

TATEM, H. E. 1977. Accumulation of naphthalenes by grass shrimp: effects on respiration, hatching, and larval growth, p. 201–209. *In* D. A. Wolfe [ed.] Fate and effects of petroleum hydrocarbons in marine ecosystems and organisms. Pergamon Press, New York, NY. 78 p.

TATTERSFIELD, F., AND H. M. MORRIS. 1924. An apparatus for testing the toxicity values of insecticides under controlled conditions. Bull. Entomol. Res. 14: 223–233.

ULLRICH, S. O. JR. 1981. The effect of temperature on the toxicity of the water soluble fractions of diesel fuel No. 2 and H-coal crude oil to *Daphnia magna*. M.S. thesis, Ohio State University, Columbus, OH. 78 p.

U.S. ENVIRONMENTAL PROTECTION AGENCY (U.S. EPA). 1977. National water quality inventory. 1976 report to Congress. EPA/440/9-76/0.24. Office of Water Planning & Standards, Washington, DC.

WELLS, P. G., AND J. B. SPRAGUE. 1976. Effects of crude oil on the American lobster *Homarus americanus* larvae in the laboratory. J. Fish. Res. Board Can. 33: 1604–1614.

WINTERS, K., R. O. DONNELL, J. C. BATTERSON, AND C. VAN BAALEN. 1976. Water soluble components of four fuel oils: chemical characterization and effects on growth of microalgae. Mar. Biol. 36: 269–276.

Evaluation of the Phosphorus–Chlorophyll Relationship for Lakes Off the Precambrian Shield in Western Canada

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PREPAS, E. E., AND D. O. TREW. 1983. Evaluation of the phosphorus–chlorophyll relationship for lakes off the Precambrian Shield in western Canada. Can. J. Fish. Aquat. Sci. 40: 27–35.

Summer chlorophyll (Chl), spring and summer total phosphorus (TP), and total nitrogen (TN) data were collected from 25 lakes off the Precambrian Shield in Alberta. Contrary to the results reported in previous studies in western Canada, the spring TP–summer Chl relationship ($n = 29$, $r^2 = 0.67$) and TN:TP ratios were similar to those reported for other north-temperate lakes. However, there was less variation in the summer TP–summer Chl relationship ($n = 34$, $r^2 = 0.81$) than in the spring TP–summer Chl relationship. This is a result of the variability in the summer TP:spring TP ratio which ranged from 0.5 to 2.9 in these lakes. In the shallow productive freshwater lakes TP concentrations increased dramatically between spring and summer (the average summer TP:spring TP ratio was 1.7), whereas in the thermally stratified freshwater lakes (most of which were partially meromictic) summer TP concentrations were much lower than spring TP concentrations (the mean ratio was 0.7). There was less chlorophyll per unit TP in saline lakes (i.e. lakes with more than 500 mg/L total dissolved solids) than in freshwater lakes.

Key words: phosphorus, chlorophyll, western lakes, saline lakes, meromictic lakes

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On a recueilli des données sur la concentration de chlorophylle (Chl) en été, sur la concentration de phosphore total (PT) au printemps et en été, ainsi que sur la concentration d'azote total (AT) dans 25 lacs situés en Alberta à l'extérieur du bouclier précambrien. Contrairement aux résultats signalés dans des études antérieures faites dans l'ouest du Canada, la relation entre la Chl en été et le PT au printemps ($n = 29$, $r^2 = 0{,}67$) de même que les rapports entre l'AT et le PT étaient semblables à ceux signalés pour d'autres lacs tempérés au Nord. Cependant, la relation entre le Chl en été et le PT en été ($n = 34$, $r^2 = 0{,}81$) montrait moins de variation que celle existant entre la Chl en été et le PT au printemps. Cela est dû aux variations du rapport entre le PT au printemps et le PT en été qui se situaient dans ces lacs entre 0,5 et 2,9. Dans les lacs d'eau douce productifs peu profonds, la concentration de PT s'est élevée énormément entre le printemps et l'été (le rapport moyen entre le PT au printemps et le PT en été était de 1,7), par contre, dans les lacs d'eau douce où il y avait une stratification thermique (la plupart d'entre eux étaient partiellement méromictiques) la concentration de PT au cours de l'été était beaucoup plus faible qu'au printemps (le rapport moyen était de 0,7). Il y avait moins de chlorophylle par unité de PT dans les lacs salins (c'est-à-dire les lacs contenant plus de 500 mg/L de solides totaux dissous) que dans les lacs d'eau douce.

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THE proportionality of phytoplankton biomass and productivity to total phosphorus concentration ([TP]) has been documented in many limnological studies (Nicholls and Dillon 1978; Smith 1979) and forms the basis of eutrophication control schemes (Dillon and Rigler 1975). This relationship between phytoplankton biomass and [TP] is robust except in lakes with low ratios of total nitrogen (TN):TP (e.g. Sakamoto 1966), although the definition of a low

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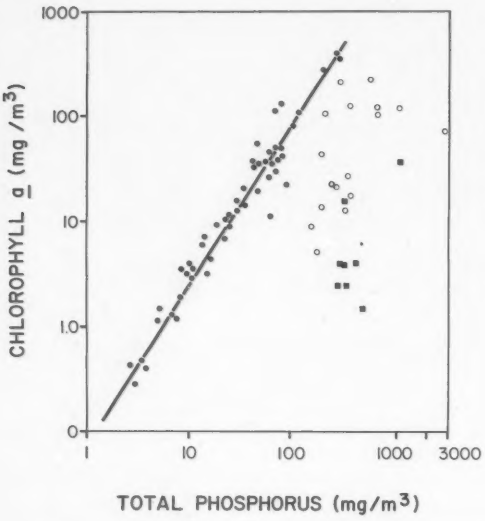

FIG. 1. Relationship between mean summer chlorophyll and total phosphorus at spring overturn. Closed circles (●), data from Dillon and Rigler (1974); squares (■), data from Gallup (1978), phosphorus was from open-water period; open circles (○), data from Hickman (1980), chlorophyll was maximum summer. The line is from Dillon and Rigler (1974).

TN:TP ratio (by weight) varies from 5 (Schindler 1977) to 13 (Smith 1979).

The productive Qu'Appelle Valley lakes in southern Saskatchewan are among those which are reported to have very low chlorophyll *a* (Chl *a*):TP and TN:TP ratios (Allan and Kenney 1978). Recent reports on central Albertan lakes (Gallup 1978; Hickman 1980) suggest that this phenomenon extends to other lakes situated off the Precambrian Shield in western Canada. Mean summer [Chl *a*] in the eight lakes studied by Gallup were only 0.3–6.0% of the values predicted by the Dillon and Rigler (1974) model from mean open water [TP] (Fig. 1). Similarly, the maximum summer [Chl *a*] in the 12 lakes described by Hickman were far less than mean concentrations predicted by the same model (Fig. 1). More than half the lakes studied by Gallup and Hickman had TN:TP ratios which were less than 5.

These data suggest that TP is in excess in this region and that lakes off the Precambrian Shield in western Canada may be nitrogen- rather than phosphorus-limited. As a result we collected data on [TP], [TN], and [Chl *a*] for 25 lakes in Alberta to determine the nature of the relationship between [TP] and/or [TN] and [Chl *a*]. We also wanted to compare the TP–Chl relationship in this study with that reported for other temperate lakes to assess whether our lakes were phosphorus-limited (Schindler 1977). From the numerous models (see Nicholls and Dillon 1978), Dillon and Rigler's (1974) was chosen because it was based on a broad range of lakes and only used data collected from May through August.

Materials and Methods

Two laboratories, the limnology laboratory at the University of Alberta and the Water Quality Control Branch of Alberta Environment participated in this study. Identical sampling methods were used by both laboratories. Most of the analyses were performed at the University of Alberta; however, where analyses were carried out in both laboratories, identical techniques were used or, if not, appropriate comparisons are given.

A preliminary study of 6 lakes was made in 1980 and these 6 lakes plus 19 new lakes were studied in 1981. The 25 lakes in this study are situated in glacial till and are located in the boreal mixed-wood and lower foothills transition biomes in central Alberta. The geographical locations are given in Table 1 (note: there are 27 entries in Table 1 because Baptiste and Amisk lakes are double-basined).

Lake surface areas were determined from 1 to 50 000 topographic maps. Bathymetric surveys were conducted on five lakes with a Furuno model FE-400 depth-sounder, and morphometric data were calculated after Hutchinson (1957). Morphometric data for the other lakes were obtained from Alberta Environment, and Alberta Energy and Natural Resources.

Lakes were sampled an average of 6 times (range 3–9) from within 2 wk of ice melt (late April) until the end of August. In situ vertical profiles of temperature and light penetration were measured on each visit at the deepest site. Temperature was measured at 1-m intervals with a resistance thermistor accurate to 0.1°C; epilimnetic, metalimnetic, and hypolimnetic zones of the water column were defined according to Hutchinson (1957). The depth of the trophogenic zone was defined as 1% of surface-penetrating irradiance as measured with a Lambda LI-185 light meter with a quantum sensor. This value was compared with twice Secchi disk depth.

The vertical distributions of dissolved oxygen, Chl *a*, and TP concentrations were determined from water samples collected at the same location. Dissolved oxygen was determined on water samples collected at 1- to 2-m intervals from the middle of the metalimnion to the bottom of the water column or until dissolved oxygen concentrations approached zero. Chlorophyll profiles were constructed from samples collected at 1-m intervals from the surface to the bottom of the trophogenic zone. Phosphorus profiles were established from samples collected at 2-m intervals in the epilimnion, 1-m intervals in the metalimnion and where dissolved oxygen concentrations approached zero, and at 5-m intervals in the hypolimnion. These discrete water samples were collected with a 1.5-L aluminium, drop-sleeve water bottle.

Mean epilimnetic and trophogenic [TN], [TP], and [Chl *a*] representative of the whole lake were determined from pooled samples collected at 3–20 stations in each lake. The number of stations sampled was proportional to lake surface area and chlorophyll concentration. Integrated samples were collected from the epilimnetic and trophogenic zones at each station using weighted Tygon tubing. At no time was the Tygon tubing allowed to go deeper than 2 m above the bottom. To avoid changes in the water samples during storage, all containers were completely filled.

Dissolved oxygen was determined on water samples which

TABLE 1. Background data for the 25 study lakes: location, surface area, mean depth ($\bar{z}$), and total dissolved solids (TDS), alkalinity, color, and turbidity in the epilimnion.

Lake	Lat.[a] (°N)	Long.[a] (°W)	Area (km^2)	$\bar{z}$ (m)	TDS (mg/L)	Alkalinity (mg/L $CaCO_3$)	Color (mg/L Pt)	Turbidity (JTU)
Amisk North	54°35′	112°37′	1.89	10.7[b]	196	162	20	3.8
Amisk South	54°35′	112°37′	2.27	19.4[b]	203	154	19	3.6
Baptiste North	54°45′	113°33′	4.74	5.9	192	150	22	5.1
Baptiste South	54°45′	113°33′	4.43	12.7[b]	195	153	25	3.4
Birch	53°45′	114°32′	7.51	4.5	188	—	—	—
Bourque	54°40′	110°33′	5.00	8.3	187	—	—	—
Cooking	53°26′	113°02′	44.3	2.4	1108	450	45	15
Eden	53°35′	114°09′	0.41	6.2	128	83	8	0.53
Ethel	54°32′	110°21′	4.83	6.6	182	164	—	—
Halfmoon	54°04′	113°21′	0.57	—	194	130	12	3.8
Hasse	53°29′	114°10′	0.81	3.2	274	—	—	—
Hastings	53°25′	112°55′	9.06	3.7	748	269	19	4.2
Hilda	54°31′	110°26′	3.62	6.2	480	—	—	—
Hubbles	53°34′	114°05′	0.45	9.9[b]	390	138	4	0.53
Joseph	53°17′	113°04′	6.68	2.4	1545	910	55	34
Marie	54°38′	110°18′	36.2	14.1	171	—	—	—
Mink	53°31′	114°14′	0.70	3.4	1186	149	5	1.0
Moore	54°31′	110°31′	9.30	8.3	476	376	5	1.9
Nakamun	53°53′	114°12′	3.16	3.5	190	125	25	22
Narrow	54°35′	113°37′	3.33	14.2[b]	190	157	8	1.0
Roi	53°35′	114°05′	0.06	8.2	412	222	5	1.0
Sauer	53°35′	114°05′	0.23	4.8	150	88	5	1.4
Star	53°31′	114°15′	0.27	3.9	694	80	30	0.05
Tucker	54°32′	110°37′	7.22	2.9	249	203	10	6.5
Twin	52°55′	114°20′	0.24	15.8[b]	209	199	12	0.05
Wizard	53°07′	113°55′	2.18	5.0	208	177	14	3.0
Wolf	54°42′	110°57′	30.6	9.5	210	—	—	—

[a]Gazetteer of Canada, Vol. 6, 1965.
[b]Calculated from morphometric data collected in this study.

were fixed in the field, chilled, and analyzed within 24 h by Carpenter's (1965) modified Winkler technique.

Total nitrogen was calculated as the sum of total Kjeldahl nitrogen (TKN), nitrite-N (NO_2), and nitrate-N (NO_3). Inorganic nitrogen was calculated as the sum of ammonia-N (NH_4), NO_2, and NO_3. Total Kjeldahl nitrogen was determined on samples which had been placed in 250-mL polystyrene containers and preserved with 0.25 mL of concentrated sulfuric acid. These samples were prefiltered through a 250-μm Nitex net (after Dillon and Rigler 1974) and digested by the sulfuric acid–copper sulfate method of D'Elia et al. (1977) with the following modifications: Hengar granules (obtained from Fisher Scientific Company, Edmonton) were used instead of glass beads, the digested samples were neutralized with a 50% solution and a 0.5% solution of NaOH, and if the pH went above 6.0, a solution of 10% sulfuric acid was added to lower it to 5.2. These samples were analyzed by Solórzano's (1969) phenolhypochlorite method. Ammonia was determined on samples which were stored in 250-mL polystyrene containers and analyzed by the method of Solórzano. Nitrate–nitrite was determined on samples which had been collected in 1-L Nalgene polyethylene bottles, filtered through prewashed 0.45-μm HAWP Millipore membrane filters, and analyzed by the cadmium–copper reduction method of Stainton et al. (1977). All samples were stored at 5°C from the time of collection and analyzed within 24 h for NH_4, and within 48 h for NO_2, NO_3, and TKN. The containers used to store water for nitrogen analyses were cleaned with double distilled water (DDW).

Total phosphorus was determined on samples which had been collected in 1-L acid-washed Nalgene bottles and within 4 h of collection prefiltered through a 250-μm Nitex net (after Dillon and Rigler) and transferred to culture tubes. They were digested and analyzed by Menzel and Corwin's (1965) potassium persulfate method as modified by Prepas and Rigler (1982). Glass culture tubes and Kjeldahl flasks used in nitrogen and phosphorus analyses were rinsed 3 times with DDW after use. All other glassware were washed in 2% HCl acid, then rinsed 4 times with distilled water and 3 times with DDW. All nitrogen and phosphorus determinations were done in triplicate.

Two techniques were used to determine [Chl *a*]. In both cases water samples were collected in opaque 1- to 2-L Nalgene bottles. Duplicate subsamples were prepared within 4 h of collection by filtering 50–500 mL of lake water, depending on cell density, through glass fiber filters. The laboratory at the University of Alberta subsequently used a spectrophotometric technique based upon the ethanol extraction procedure of Ostrofsky (unpublished) described by Bergman and Peters (1980). Sample filters, which had been rinsed with 1 mL of a saturated $MgCO_3$ solution, were placed in sealed petri dishes, protected from light with aluminium foil, and frozen. Analysis was completed within 2 wk of collection. The laboratory at Alberta Environment used the

TABLE 2. Nutrient and chlorophyll data and the thermal characteristics for the 25 study lakes: summer thermal regime (S, stratified; M, isothermal), spring total phosphorus (TP), mean summer chlorophyll *a* (Chl *a*), mean summer trophogenic TP, mean summer epilimnetic TP, mean summer epilimnetic TP:spring TP ratio, total nitrogen (TN):TP ratio in spring, and TN:TP ratio for the trophogenic zone in summer. Data for lakes studied in 1980 and 1981 are presented in chronological order.

Lake		Spring [TP] (mg/m^3)	Summer [Chl *a*] (mg/m^3)	Summer trophogenic [TP] (mg/m^3)	Summer epilimnetic [TP] (mg/m^3)	Summer epilimnetic TP / Spring TP	Spring TN:TP	Summer trophogenic TN:TP
Amisk North	S	66.0	21.6	37.9	36.8	0.56	—	—
		—	18.3	31.6	31.7	—	—	54
Amisk South	S	68.7	21.0	38.6	37.4	0.54	—	—
		—	20.7	33.0	32.0	—	—	40
Baptiste North	M	57.8	34.1	65.6	—	1.13[a]	—	—
		—	34.8	46.2	44.5	—	—	31
Baptiste South	S	79.9	50.9	55.3	48.8	0.61	—	—
		—	26.0	38.0	34.4	—	—	37
Birch	M	45.2	21.7	53.8	—	1.19[a]	33	25
Bourque	S	16.4	4.8	19.1	17.1	1.04	49	37
Cooking	M	303	158	274	—	0.90[a]	14	29
Eden	S	28.7	9.2	19.6	16.2	0.56	37	36
Ethel	S	34.6	6.3	19.9	19.0	0.55	22	44
Halfmoon	M	—	46.2	95.8	—	—	—	29
Hasse	M	27.0	3.3	21.4	21.4	0.79	53	54
Hastings	M	152.0	80.6	156	158	1.03[a]	13	27
Hilda	S	28.3	5.6	25.7	22.2	0.78	43	44
Hubbles	S	27.1	10.4	—	15.8	—	—	—
		26.2	7.6	20.7	20.3	0.77	39	50
Joseph	M	761	89.0	755	—	0.99[a]	5	9
Marie	S	15.8	5.5	16.0	13.8	0.87	49	40
Mink	M	24.7	5.3	26.9	26.6	1.09[a]	49	39
Moore	S	33.9	4.7	23.6	22.4	0.66	29	48
Nakamun	M	53.1	41.7	155	150	2.92[a]	—	—
		78.4	150	155	124	1.98[a]	18	20
Narrow	S	—	2.2	12.5	12.2	—	—	—
		11.1	3.4	11.8	10.1	0.91	51	45
Roi	S	13.4	5.8	14.8	9.8	0.73	62	64
Sauer	S	33.0	18.6	31.7	18.3	0.55	39	38
Star	S	28.8	5.4	21.2	20.8	0.72	40	50
Tucker	M	29.1	30.0	58.9	53.4	2.02[a]	32	18
Twin	S	21.4	1.7	12.0	11.7	0.55	—	—
		16.3	2.3	12.8	9.6	0.59	22	26
Wizard	M	36.3	26.4	44.2	45.6	1.22[a]	26	25
Wolf	S	39.4	7.3	21.3	19.7	0.50	24	41

[a]Summer [TP] in the trophogenic zone used in ratio.

fluorometric procedure using acetone extraction of Yentsch and Menzel (1963) as modified by Holm-Hansen et al. (1965). Sample filters were placed directly in acetone and refrigerated in the dark; analyses were completed within 1 wk.

Although differences between the fluorometric and spectrophotometric techniques have been reported (Cullen 1982), we found no evidence of significant disagreement between the two techniques even though only the fluorometric procedure employed a pheophytin correction. The fluorometric technique was used for samples collected from 10 lakes in this study. To compare the two methods 29 duplicate sets of samples were collected from these 10 lakes and analyzed by both techniques. The results, which ranged from 3 to 68 mg/m^3 Chl *a*, were highly correlated ($r^2 = 0.99$, $P < 0.0001$) and there was no evidence that one method gave results which were consistently higher or lower than the other method (paired *t*-test, $P > 0.5$).

Total dissolved solids, alkalinity, color, and turbidity were determined during the summer of 1981 on epilimnetic water samples which were collected in 1-L acid-washed Nalgene bottles. Samples were stored at 5°C from time of collection and were analyzed within 48 h. Total dissolved solids was determined on 50 mL of water if conductivity was greater than 500 μmho/cm, or 100 mL of water if less than 500 μmho/cm. The samples were filtered through washed 0.45-μm HAWP membrane filters and placed in a preweighed porcelain evaporating dish. They were then evaporated at 105°C for 16 h, cooled in a desiccator, and reweighed. Total dissolved solids were calculated as outlined in Stainton et al. (1977). Alkalinity was determined by the potentiometric titration method of Environment Canada (1979). Color was measured visually, after samples were centrifuged for 10 min,

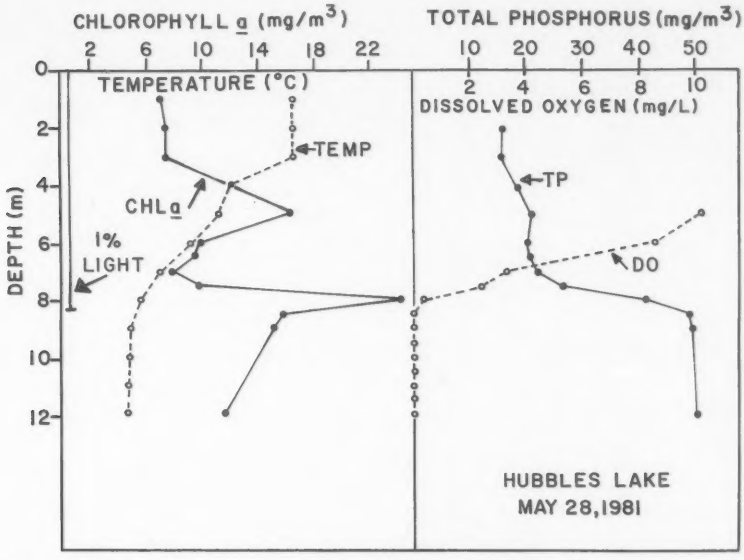

FIG. 2. An illustration of the vertical stratification of chemical parameters in a partially meromictic lake: vertical distribution of dissolved oxygen (DO), total phosphorus (TP), temperature (temp), chlorophyll *a* (Chl *a*), and the depth to where 1% light penetrated, Hubbles Lake, May 28, 1981.

on a Hazen platinum–cobalt scale with a Hellige aqua tester model 611A. Turbidity was measured using a Hach turbidimeter model 2100A.

To estimate empirical relationships we used linear and stepwise multiple regression analyses on data which were transformed to $\log_{10}$ (see Snedecor and Cochran 1980).

Results

General Characteristics of the Study Lakes

The study lakes are similar to many off-Shield lakes in western Canada, east of the Rocky Mountains (Rawson and Moore 1944) (see Tables 1 and 2). The total dissolved solids range from 128 to 1545 mg/L, and on this basis the lakes can be classified as either freshwater (TDS < 500 mg/L) or saline (TDS > 500 mg/L) (Rawson 1951). The lakes are not heavily colored (4–55 mg/L platinum), are alkaline (80–910 mg/L $CaCO_3$), and most are not very turbid [0.1–34 Jackson Turbidity Units (JTU)]. The study lakes encompass a wide range of sizes (surface areas 0.06–36 km^2), depths (mean depths 2.4–19 m), and mixing patterns. During the open-water season 10 lakes were continuously mixed and 15 were stratified. However, profiles of total dissolved solids, temperature, and dissolved oxygen revealed that 13 of the 15 stratified lakes were partially meromictic and another lake, Roi Lake, was permanently meromictic.

Low or non-detectable dissolved oxygen levels and correspondingly high total phosphorus values were recorded in the hypolimnia of these stratified lakes, and deep chlorophyll peaks were observed in the less productive lakes. These vertical gradients are illustrated by data collected on Hubbles Lake, a small (surface area 0.5 km^2) and relatively deep (maximum depth 30 m) lake. This lake did not mix completely in the spring and fall of 1980, or in the spring of 1981. As a result, in early May 1981 at 8 m, TP increased threefold and below 8 m there was no detectable dissolved oxygen (Fig. 2). Moreover, later in May two chlorophyll maxima developed, one in the metalimnion and a second at the depth where dissolved oxygen levels approached zero (Fig. 2). Deep chlorophyll maxima were also observed in five other lakes in this study (Eden, Narrow, Roi, Sauer, and Twin). In these lakes, an average of 80% of the trophogenic chlorophyll (m^{-2}) was found below the epilimnion. These deep chlorophyll maxima may develop in response to high nutrient and adequate light levels (Fee 1976). It is also possible that some of this deep chlorophyll is pheophytin; however, this parameter was not estimated in these lakes.

There were an unusually high number of meromictic lakes in this study. This was puzzling because these lakes were neither exceptionally deep relative to their surface areas nor well protected from the prevailing winds. The widespread meromixis may, however, be induced by the relatively low wind speeds in central Alberta. Mean monthly wind speeds for Edmonton (Alberta) were consistently less than for Regina (Saskatchewan), Windsor and Simcoe (Ontario), and Schefferville (Quebec) as determined from meteorological summaries (Fisheries and Environment Canada 1977–1980a, b). High wind power above lakes during spring and fall is an important factor in overturn (Stauffer 1980).

Inputs to the TP–Chl Model

As we were planning to compare the TP-Chl relationship

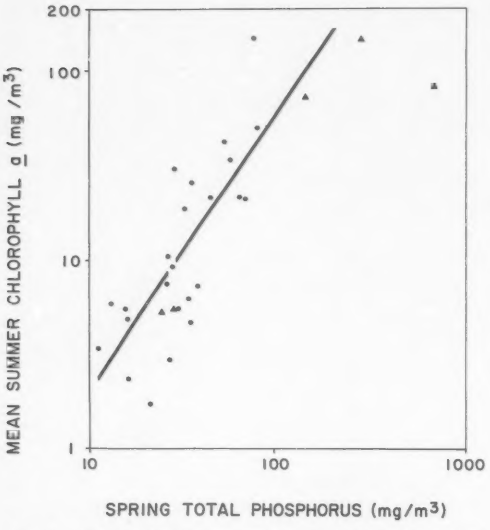

FIG. 3. Relationship between mean summer chlorophyll and total phosphorus at spring overturn in lakes in central Alberta. Triangles (▲), saline lakes. The line is from Dillon and Rigler (1974).

in our lakes with Dillon and Rigler's (1974) model, we attempted to keep our methods and periods of collection as similar to theirs as possible. Dillon and Rigler's model has two variables, spring [TP] and mean summer [Chl *a*] in the trophogenic zone. They assumed that (1) [TP] was homogeneous throughout the water column at spring overturn; (2) there was a clear division between spring overturn and summer stratification; (3) the Secchi disk could estimate the trophogenic zone; and (4) in summer all water in the trophogenic zone was suitable for algal production. However, these assumptions did not hold for the lakes in this study.

Variables in the TP–Chl model were therefore modified in four ways to accommodate the conditions in the study lakes. (1) Because there was no method to determine whether phosphorus in anoxic water was available for the production of summer algal biomass, spring [TP] was calculated only from water collected in the portion of the water column which had detectable levels of dissolved oxygen. (2) The transition from spring to summer is usually defined as the onset of permanent thermal stratification. This general definition was not used because 10 lakes in the study did not stratify permanently during the summer period and 14 more were stratified from ice-out. Spring was thus arbitrarily defined as the period from ice-out until the end of the 3rd week in May, and summer from the beginning of the 4th week in May until the end of August. (3) The Secchi disk is traditionally used to define the trophogenic zone, but in this study the light meter proved to be more accurate. The depth of the trophogenic zone differed depending on whether it was defined by a Secchi disk or light meter; the ratio varied from 0.8 to 2.4. The discrepancies were most noticeable for lakes with deep chlorophyll maxima and the shallow productive lakes. (4) Because algal production is usually limited to water with detectable levels of dissolved oxygen, the portion of the trophogenic zone containing anoxic water was excluded from the integrated summer samples.

PHOSPHORUS–CHLOROPHYLL RELATIONSHIPS IN LAKES IN WESTERN CANADA

The relationship between spring [TP] and mean summer [Chl *a*] derived for the lakes in this study was similar to that predicted by Dillon and Rigler's model. The data are evenly scattered above and below Dillon and Rigler's regression line ($\chi_c^2 = 0.14$, $P > 0.5$) (Fig. 3). We thus found no evidence that lakes in western Canada produce consistently less chlorophyll per unit phosphorus than other temperate lakes. The TP–Chl relationship in our lakes (Table 2) was:

(1) $\log [\text{Chl } a] = -0.676 + 1.119 \log [\text{TP}]\text{sp}$

($n = 29$, $r^2 = 0.67$), where [TP]sp is spring [TP]. There were two differences between this relationship and Dillon and Rigler's model:

(2) $\log [\text{Chl } a] = -1.136 + 1.448 \log [\text{TP}]\text{sp}$

($n = 46$, $r^2 = 0.90$). Equation 1 accounts for significantly less variation than Eq. 2 (two-tailed F-test, $P < 0.05$). Secondly, the slope in Eq. 1 is much lower than in Eq. 2, although this difference could not be tested statistically as a result of variance heterogeneity. These differences, which will be discussed in detail below, appear to be a function of the properties of lakes in western Canada.

One factor which could explain the high variance of the data used for Eq. 1 is the variability in the relationship between spring and summer [TP] in these lakes. It is often assumed that there are only small seasonal changes in within-lake [TP] (Dillon and Rigler 1974) with spring [TP] slightly higher than either mean summer (Nicholls and Dillon 1978) or mean annual [TP] (Chapra and Tarapchak 1976). The mean summer [TP]:spring [TP] ratio in 12 lakes studied by Dillon and Rigler, was 0.87 and this relationship was quite consistent ($r^2 = 0.92$, Nicholls and Dillon 1978). However, the summer [TP]:spring [TP] ratio in this study was not at all consistent, varying from 0.5 to 3.0 (Table 2).

Although our lakes form a continuum with respect to the summer TP:spring TP ratio, they can be roughly divided into three groups: the shallow productive freshwater lakes (i.e. do not permanently stratify in summer, mean summer [Chl *a*] is greater than 10 mg/m^3, and have less than 500 mg/L total dissolved solids), the shallow saline lakes (i.e. do not permanently stratify in summer and have more than 500 mg/L total dissolved solids), and the other lakes (most of which had permanent thermal stratification in summer).

The summer [TP] in the shallow productive freshwater lakes, (i.e. Baptiste N., Birch, Nakamun, Tucker, and Wizard) was higher than spring [TP] and fluctuated dramatically, as illustrated in Fig. 4 with data from Nakamun Lake. In this group the average summer TP:spring TP ratio was 1.74 (range 1.2–2.9, Table 2). However, in the shallow saline lakes (i.e. Cooking, Hastings, Joseph, and Mink), the [TP] remained fairly stable throughout the study period and there was apparently no significant change in [TP] between spring and summer. The average summer TP:spring TP ratio

for these lakes was 1.00 (range 0.9–1.1, Table 2). However, most of the stratified lakes had mean summer TP levels which were lower than spring values although the changes in [TP] in these lakes were fairly gradual, as illustrated in Fig. 4 with data from Twin Lake. The average summer TP:spring TP ratio for these lakes ($n = 18$) was 0.68 (range 0.50–1.04, Table 2). Thus three quite distinct patterns of seasonal TP levels were observed.

The seasonal fluctuations in trophogenic [Chl *a*] paralleled those of [TP] in most cases. This was shown by fitting regression lines to paired measurements of summer trophogenic TP and chlorophyll levels for each lake which had three or more pairs of points per summer. Because the number of points used to construct each regression line was too small (i.e. 3–7) to test the significance of individual lines, the probabilities were combined following a technique outlined in Sokal and Rohlf (1981, Box 18.1). Total phosphorus and chlorophyll levels were correlated during summer on a day-to-day basis within lakes (χ^2 test, $P < 0.025$).

This correlation between paired measurements of [TP] and [Chl *a*] in individual lakes implies that summer [TP] rather than spring [TP] should be the best predictor of summer chlorophyll when there is substantial variation in the seasonal patterns of [TP]. The summer TP–Chl relationship (Table 2) was:

$$(3)\quad \log [\text{Chl } a] = -0.661 + 1.146 \log [\text{TP}]\text{su}$$

($n = 34$, $r^2 = 0.81$) where [TP]su is mean summer trophogenic [TP]. Although the slope of Eq. 3 is similar to Eq. 1, the variation around Eq. 3 is much less than for Eq. 1 and is not different from Dillon and Rigler's model (two-tailed F-test, $P > 0.5$).

A portion of the variance in Eq. 1 could also be caused by poor chlorophyll estimates for the productive lakes. Spatial and temporal fluctuations in chlorophyll were greatest in these lakes. The sampling program was not, however, adjusted to accommodate all of these fluctuations because sufficient baseline data were not available. An intensive study of the chlorophyll fluctuations in productive lakes is required to design better sampling programs for these lakes and to evaluate the data presented here.

The lower slope in Eq. 1 as compared to Eq. 2 could be caused by the presence of saline lakes. In this study there were five saline lakes (Cooking, Hastings, Joseph, Mink, and Star), all with relatively low Chl:TP ratios (Fig. 3), whereas there were no saline lakes in Dillon and Rigler's study. Additionally, Joseph Lake, which showed the greatest deviation from Eq. 1, was the most saline. When the saline lakes were removed, the TP–Chl relationship was:

$$(4)\quad \log [\text{Chl } a] = -1.327 + 1.573 \log [\text{TP}]\text{sp}$$

($n = 24$, $r^2 = 0.63$). The slope of Eq. 4 is higher than our original equation (Eq. 1), and very similar to Eq. 2 (t-test, $P > 0.5$). Although the sample size is very small, this is evidence that saline lakes have lower Chl:TP ratios than freshwater lakes. More saline lakes should be studied to determine whether this ratio is consistently low.

The three most productive saline lakes, Cooking, Hastings, and Joseph, also had low TN:TP ratios in spring: 13, 14, and 5, respectively. However, the TN:TP ratios in these three lakes doubled during the summer; the corresponding mean summer ratios were 29, 27, and 9 (Table 2). Thus only the summer TN:TP ratio in Joseph was low, although it is not considered a low ratio in the view of some investigators (e.g. Schindler 1977). Joseph not only had the lowest TN:TP ratio, but also had the highest dissolved solids and turbidity levels (Table 1), and thus was an outlier in several ways. When Joseph was excluded from Eq. 1, the slope of the equation increased, but was still lower than in Dillon and Rigler's model (Eq. 2). It is difficult to understand why the Chl:TP ratio is so low in this lake. It could be due to a combination of factors: the low TN:TP ratio, high light extinction caused by high turbidity, and the high level of dissolved solids.

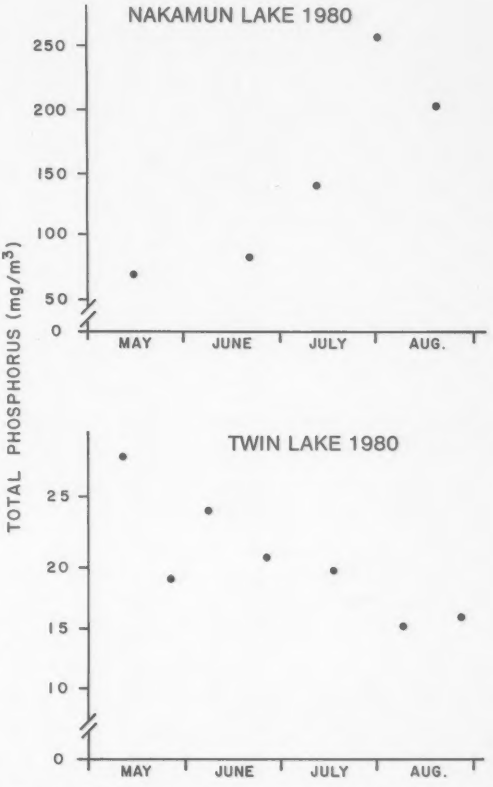

FIG. 4. Total phosphorus concentration in the trophogenic zone of a shallow lake, Nakamun, and a deep lake, Twin, from May until August 1980.

NITROGEN–CHLOROPHYLL RELATIONSHIP IN LAKES IN WESTERN CANADA

Total nitrogen and mean summer chlorophyll were highly correlated in this study (Table 2), the r^2 was 0.57 for the spring TN–Chl relationship and 0.74 for the summer

TABLE 3. A comparison of total phosphorus concentrations ([TP]) mg/m^3) reported by Gallup (1978) and Hickman (1980) and data collected in this study in 10 Albertan lakes.

Lake	Gallup mean [TP]	Hickman spring [TP]	This study: Spring [TP]	This study: Mean summer [TP]
Buffalo	400	300[a]	—	62
Cold	270	170	—	15
Cooking	1100	455[a]	303	274
Gull	300	325[a]	—	44
Hastings	—	630	152	156
Joseph	—	2880	761	755
Miquelon	480	1040	—	172
Moose	300	230[a]	—	32
Pigeon	280	165[a]	—	32[b]
Sylvan	320	240	—	22

[a]Average for 2 yr.
[b]Datum provided by H. Hamilton and T. Reynoldson (Alberta Environment).

TN−Chl relationship. However, these correlations were weaker than for the corresponding TP−Chl relationship ($r^2 = 0.67$ and 0.81, respectively). When TN and TP were used in a multiple regression to predict chlorophyll, TN did not add more information than TP alone (t-tests, $P > 0.4$) as TN and TP were highly correlated (e.g. the r^2 for mean summer values was 0.86). Inorganic nitrogen did not follow the same pattern as TN. There was no significant relationship between either spring or summer inorganic nitrogen in the trophogenic zone and mean summer chlorophyll (t-tests, $P > 0.25$). Thus, as also noted in other studies (Smith 1979), nitrogen has less predictive power for chlorophyll biomass than total phosphorus.

Discussion

Not only was the TP−Chl relationship in our study lakes similar to those reported for lakes on the Precambrian Shield (Dillon and Rigler 1974), but the TN:TP ratios were also similar. The mean TN:TP ratio in spring was 34, and in the trophogenic zone in summer it was 37. Both the Chl:TP and the TN:TP ratios are, however, much higher than those reported by Gallup (1978) and Hickman (1980) for lakes in the same area, and in three cases, for the same lakes.

We investigated whether these differences were caused by poor estimates of [TP] in the previous studies. Water samples were analyzed for [TP] from seven of the lakes studied by Gallup and Hickman in addition to the three included in this study. In all cases our [TP] values were lower than Gallup and Hickman's (Table 3). The differences range from twofold to more than an order of magnitude. These differences are due to the analytical methods used by Gallup and Hickman. Their standards were prepared as phosphate rather than phosphorus standards, i.e. for a standard solution of 10^5 mg P/m^3 they used 0.143 rather than 0.439 g KH_2PO_4 dissolved in 1 L of DDW (G. Hutchinson, Department of Zoology, University of Alberta, personal communication). Total phosphorus concentrations calculated from their standards are thus overestimated by a factor of 3. In addition, containers and glassware used for analyses of Gallup and Hickman's samples were washed with Alconox, a detergent containing several parts per hundred phosphorus (G. Hutchinson personal communication). This detergent caused a high degree of contamination in Gallup and Hickman's samples and explains why the differences between their data and ours were not simply threefold.

We cannot explain why Allan and Kenney's (1978) TN:TP and Chl:TP ratios were so similar to Gallup and Hickman's. However, the Qu'Appelle Valley lakes are saline; total dissolved solids ranged from 887 to 1285 mg/L (Rawson and Moore 1944). If saline lakes generally produce less chlorophyll than freshwater lakes, then these lakes would be expected to have low Chl:TP ratios.

The close correlation between levels of TP and Chl a and the high TN:TP ratios found in this study suggest that phosphorus is the nutrient controlling the level of phytoplankton productivity in western Canadian lakes. This study also suggests that dividing the lakes into three categories (shallow productive, thermally stratified, and saline) would improve the correlation between spring [TP] and summer [Chl]. However, much more information needs to be collected on these lakes before comprehensive eutrophication control schemes can be developed. In particular, the seasonal fluctuations of [TP] in the shallow productive lakes and the drop in TP levels during the summer in the thermally stratified lakes need further investigation. It is also important to explore when and to what extent high levels of total dissolved solids are associated with low phytoplankton biomass.

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ALLAN, R. J., AND B. C. KENNEY. 1978. Rehabilitation of eutrophic Prairie lakes in Canada. Verh. Int. Verein. Limnol. 20: 214−224.

BERGMANN, M., AND R. H. PETERS. 1980. A simple reflectance method for the measurement of particulate pigment in lake water and its application to phosphorus−chlorophyll−seston relationships. Can. J. Fish. Aquat. Sci. 37: 111−114.

CARPENTER, J. H. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnol. Oceanogr. 10: 141−143.

CHAPRA, S. C., AND S. J. TARAPCHAK. 1976. A chlorophyll a model and its relationship to phosphorus loading plots for lakes. Water Resour. Res. 12: 1260−1264.

CULLEN, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll a. Can. J. Fish. Aquat. Sci. 39: 791−803.

D'ELIA, C. F., P. A. STEUDLER, AND N. CORWIN. 1977. Deter-

mination of total nitrogen in aqueous samples using persulfate digestion. Limnol. Oceanogr. 22: 760–764.

DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. J. Fish. Res. Board Can. 32: 1519–1531.

ENVIRONMENT CANADA. 1979. Analytical methods manual. Inland Water Directorate. Water Quality Branch, Ottawa, Can.

FEE, E. J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: implications for primary production estimates. Limnol. Oceanogr. 21: 767–783.

FISHERIES AND ENVIRONMENT CANADA. 1977–1980a. Monthly Record: Meteorological observations in western Canada. Vol. 62 -65.

1977–1980b. Monthly Record: Meteorological observations in eastern Canada. Vol. 62–65.

GALLUP, D. N. 1978. Lakes of central Alberta with emphasis upon Moose Lake. Verh. Int. Verein. Limnol. 26: 182–189.

HICKMAN, M. 1980. Phosphorus, chlorophyll and eutrophic lakes. Arch. Hydrobiol. 88: 137–145.

HOLM-HANSEN, O., C. LORENZEN, R. W. HOLMES, AND J. D. H. STRICKLAND. 1965. Fluorometric determinations of chlorophyll. J. Cons. Cons. Perm. Int. Explor. Mer 30: 3–15.

HUTCHINSON, G. E. 1957. A treatise on limnology. 1. Wiley, New York, NY. 1015 p.

MENZEL, D. W., AND N. CORWIN. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound factions by persulfate oxidation. Limnol. Oceanogr. 10: 280–282.

NICHOLLS, K. H., AND P. J. DILLON. 1978. An evaluation of phosphorus–chlorophyll–phytoplankton relationships for lakes. Int. Rev. Gesamten Hydrobiol. 63: 141–154.

PREPAS, E. E., AND F. H. RIGLER. 1982. Improvements in quantifying the phosphorus concentration in lake water. Can. J. Fish. Aquat. Sci. 39: 822–829.

RAWSON, D. S. 1951. The total mineral content of lake waters. Ecology 32: 669–672.

RAWSON, D. S., AND J. E. MOORE. 1944. The saline lakes of Saskatchewan. Can. J. Res. D, 22: 141–201.

SAKAMOTO, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. Arch. Hydrobiol. 62: 1–28.

SCHINDLER, D. W. 1977. Evolution of phosphorus limitation in lakes. Science 195: 260–262.

SMITH, V. H. 1979. Nutrient dependence of primary productivity in lakes. Limnol. Oceanogr. 24: 1051–1064.

SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods. 7th ed. Iowa State Univ., IA.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. Freeman.

SOLÓRZANO, L. 1969. Determination of ammonia in natural waters by phenolhypochlorite method. Limnol. Oceanogr. 14: 799–801.

STAINTON, M. P., M. J. CAPEL, AND F. A. J. ARMSTRONG. 1977. The chemical analysis of freshwater. 2nd ed. Fish. Environ. Can. Misc. Spec. Publ. 25: 180 p. (Available from the Freshwater Institute, Winnipeg, Man.)

STAUFFER, R. E. 1980. Windpower time series above a temperate lake. Limnol. Oceanogr. 25: 513–528.

YENTSCH, C. S., AND D. W. MENZEL. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res. 10: 221–231.

Zooplankton Diversity and Biomass in Recently Acidified Lakes[1]

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CONFER, J. L., T. KAARET, AND G. E. LIKENS. 1983. Zooplankton diversity and biomass in recently acidified lakes. Can. J. Fish. Aquat. Sci. 40: 36–42.

Ten small headwater lakes in the Adirondack Mountains of New York State and 10 in the White Mountains of New Hampshire were examined for possible effects of acidification on zooplankton. The results showed that acidification, or some close correlate, had a significant negative effect on zooplankton diversity and biomass. A loss of 2.4 species of zooplankton and 22.6 mg dry wt/m^2 was correlated with each unit decrease in pH. These results, in contrast to some previous work, show a continuous decrease in diversity and biomass over the entire range of pH in the sampled lakes, 4.5–7.2. Cladocera, with the exception of *Holopedium* and *Polyphemus*, and *Epischura lacustris*, *Mesocyclops edax*, and *Cyclops scutifer*, were abundant at higher pH values but rare or absent at pH values less than 5. *Diaptomus minutus* was predominant at pH values less than 5.

Key words: acid rain, lakes, Adirondack Mountains, White Mountains, zooplankton, Cladocera, *Epischura*, *Mesocyclops*, *Cyclops*, *Diaptomus*

CONFER, J. L., T. KAARET, AND G. E. LIKENS. 1983. Zooplankton diversity and biomass in recently acidified lakes. Can. J. Fish. Aquat. Sci. 40: 36–42.

On a étudié 10 petits lacs de débit d'amont dans les montagnes Adirondack de l'état de New York et 10 autres dans les montagnes Blanches du New Hampshire, dans le but de découvrir l'incidence possible de l'acidification sur le zooplancton. Les résultats montrent que l'acidification, ou un autre facteur semblable, a une incidence négative significative sur la diversité et la biomasse du zooplancton. Une perte de 2,4 espèces de zooplancton et de 22,6 mg de poids sec/m^2 a été mise en corrélation avec chaque baisse d'une unité du pH. Ces résultats, contrairement à des travaux antécédents, montrent une diminution continue de la diversité et de la biomasse sur toute la variation de pH dans les lacs échantillonnés, soit 4,5 à 7,2. Les cladocères, sauf *Holopedium*, *Polyphemus*, *Epischura lacustris*, *Mesocyclops edax* et *Cyclops scutifer*, étaient abondants aux pH plus élevés, mais rares ou absents à un pH inférieur à 5. Au contraire, *Diaptomus minutus* était prédominant à un pH inférieur à 5.

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A negative relationship between zooplankton species diversity and lake pH has been reported for Scandinavian countries (e.g. Almer et al. 1974; Hendrey and Wright 1975; Raddum et al. 1980), for Canada (Sprules 1975a; Roff and Kwiatkowski 1977; Yan and Strus 1980), for parts of Great Britain (Fryer 1980), and for Florida (Crisman et al. 1980). With the exception of Fryer, these studies present evidence that the low pH of some lakes is a recent condition associated with acid rain (pH < 5.6). In some previous studies (Sprules 1975a; Roff and Kwiatkowski 1977) an effect of pH on zooplankton was not noted until lake pH dropped below values in the range of mid to low 5. Our survey was conducted to determine if similar effects on zooplankton have occurred in acidified lakes in mountainous regions of the northeastern United States. We sampled 10 lakes for zooplankton in both the White Mountains of New Hampshire and the Adirondack Mountains of New York during July and August of 1979 (Appendix A). Our results indicate that recent acidification, or some close correlate of acidification, has had a strong effect on both zooplankton diversity and zooplankton biomass. These effects were observed to be a continuous function of pH over a wide spectrum of pH values.

Methods

All lakes were sampled twice for limnetic macro-

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TABLE 1. Pearson's correlation coefficient. Values above 0.444 are significant at the 5% level (df = 18) and are signified by *. Values above 0.561 are significant at the 99% level and are signified by **.

	pH	Longitude	Latitude	Elevation	Area	Secchi depth	Biomass	Depth
No. species	0.886**	−0.101	0.385	−0.227	0.585**	0.087	0.308	0.229
pH		−0.002	0.341	−0.185	0.515*	0.106	0.323	0.176
Longitude			−0.380	0.580**	0.244	−0.414	−0.450*	−0.589**
Latitude				−0.090	0.088	0.338	0.077	0.339
Elevation (m)					−0.091	−0.205	−0.401	−0.340
Area (ha)						−0.218	−0.106	−0.174
Secchi depth (m)							0.005	0.726**
Biomass (mg dry wt·m^{-2})								0.286

zooplankton, once during July and once during August of 1979. Samples were collected with a 3-L transparent van Dorn sampler from three stations for each lake. Depending on maximum lake depth, samples were taken at three to five depths for a total volume of 54−90 L, and were concentrated by the procedure described by Likens and Gilbert (1970). For all lakes as a minimum a sample was collected from 0.5 m, just above the metalimnion and in the metalimnion. We counted all of the resultant 1000−8000 zooplankton per lake. All littoral and semibenthic species were excluded from our analyses, except for *Chaoborus* which migrates vertically into the limnetic zone. All observed species are reported in Appendix B. In several cases a species was represented by one or two specimens. Such very rare species probably play a minor role in major functions such as nutrient recycling and energy transfer. In subsequent discussion the expression, species number, refers to species whose relative abundance was greater than 0.1%.

We chose lakes that were as nearly alike as possible in all respects except pH. Recent pH determinations for many Adirondack lakes (C. L. Schofield, Cornell University, personal communication) allowed us to select lakes with a broad range of pH values: high values from watersheds containing carbonate outcrops and low values from watersheds lacking carbonate-rich basins. All lakes were headwater lakes, and all were thermally stratified, at least in July. Lake Constance, Black Pond, and to a lesser degree, Upper Hall Lake, all in New Hampshire, were the only lakes with a humic appearance. The lakes were at moderate altitudes, ranging between 470 and 900 m with the exception of Mirror Lake at 220 m in the Hubbard Brook Valley of New Hampshire. For New Hampshire lakes pH measurements were made on a sample collected at 0.5 m and transported in a 500-mL brown bottle, stored during transport in a van Dorn sampler filled with hypolimnetic water, and measured within 4 h on a Beckman pH meter.

Statistical analyses were performed with programs for SPSS (Nie et al. 1975). In this program the simultaneous, multiple regression treats each variable as if it has been added to the regression equation after all the other variables have been included. The stepwise, multiple regression attributes each increment in the explained sum of squares to the variable added at that step.

Biomass was estimated from length measurements obtained from samples pooled by depth for the three stations and for each collection date. We used the length-to-weight equations of Burns (1969) for length categories of the various species of *Daphnia*. *Daphnia*, *Diaphanasoma*, and copepodites of calanoids and cyclopoids were sorted into three length categories while being counted. One mean length value was used for *Bosmina*, nauplii, and rare species in our samples such as *Holopedium* and *Polyphemus*. Length was determined with an ocular micrometer at 25× for 20 individuals in each length category. For another classification of the Bosminidae see Deevey and Deevey (1971).

Results

The pH values from the 1930s or early 1950s, or both, were collected for lakes in New Hampshire by the New Hampshire Fish and Game Department (Appendix A). Seven of the lakes we sampled showed a decrease of at least 0.4 pH units with a mean decrease of 0.7 pH units. Three of the lakes showed a change of no more than 0.2 pH units between the early measurements and present-day values. The difference between these two groups may have occurred because of difference in the buffering capacity in these lakes. Many lakes in the Adirondack Mountains have also decreased in pH from the 1930s to today (Pfeiffer and Festa 1980). Many of the lakes above 610 m which once supported trout are now too acidic to do so (Schofield 1976). Unfortunately, there are practically no published records of zooplankton species distribution from the 1930s to 1960s for lakes above 610 m for either the White Mountains or the Adirondack Mountains. With two exceptions, our study cannot document a change in species composition, but can only correlate existing species distribution with pH and other variables.

The number of zooplankton species is strongly related to pH. Of the 10 lakes with a pH equal to or above 5.9, nine lakes had seven or more species, but of the 10 lakes with a pH below 5.9, only 1 had seven or more species ($\chi^2 = 12.80$, $P < 0.01$, df = 1). Of several tested variables in Table 1, species number correlated only with pH and lake area. The lack of a correlation of the number of species with longitude suggests that the relationship shown in Fig. 1 is a general characteristic of the type of lakes we sampled for both mountainous regions.

In our samples the number of species appears to rise continuously throughout the observed range of pH. This relation differs from a similar study by Sprules (1975a) on the zooplankton communities in 47 lakes in the La Cloche Mountains about 75 km southwest of Sudbury, Ont. Sprules suggested that zooplankton communities retained their diversity down to

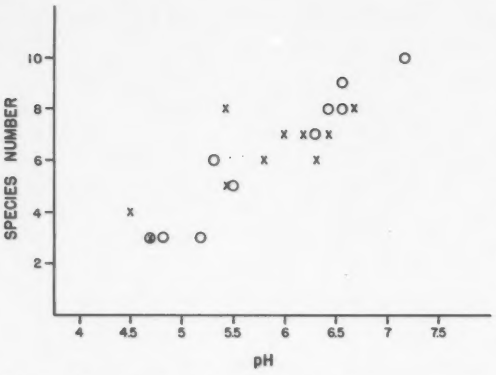

FIG. 1. The relation between pH and number of species of limnetic macrozooplankton whose numerical abundance exceeds 0.1%. Lakes from the Adirondack Mountains are represented by (o) and lakes from the White Mountains are represented by (x).

a pH of 5.0, although inspection of his data suggests that the lower limit for undisturbed community structure might be closer to a pH of 5.2. Furthermore, Roff and Kwiatkowski (1977), also studying the La Cloche Mountain lakes, estimated the Shannon and Weaver (1949) diversity index of samples from several dates for each of six lakes. Unlike our study and that of Sprules, Roff and Kwiatkowski enumerated rotifer species as well as the macrozooplankton. Roff and Kwiatkowski found that the diversity curve leveled off at about pH 5.5 which is quite similar to Sprules' results, but again contrasts with our results.

A further difference between our results and studies of the La Cloche Mountain lakes involves the rate of loss of species as pH decreases. Sprules (1975b) found a loss of 3.4 macrozooplankton species per unit decrease in pH using a stepwise, multiple regression with the three significant variables of pH, lake size, and lake depth. For comparison we have also calculated the stepwise, multiple regression of species number with all variables listed in Table 1. For all species the only significant variables were pH (F ratio = 39.2, $P < 0.01$, df = 1,17) and elevation (F ratio = 12.8, $P < 0.01$, df = 1,17). The loss rate for all species was only 1.6 per pH unit. For species number the only significant variable was pH (F ratio = 65.9, $P < 0.01$, df = 1,18) with a loss rate of 2.4 species. Our lower loss rate compared to Sprules' (1975b) results over the same pH range is associated with a lower maximum species number in our lakes.

These differences raise the question of the equivalency of sampling in Sprules' (1975a, b) study and in our study. Sprules probably sampled a larger volume and number of zooplankton. However, we did enumerate a sample of 1000–8000 zooplankton per lake. Furthermore, our procedures did detect all common macrozooplankton found in the well-studied Mirror Lake (e.g. Makarewicz and Likens 1975) and even detected a mangled *Daphnia* which was recognizable as a different species but not identifiable and which was not mentioned by Makarewicz and Likens (1975). A final observation attesting to the similarity of thoroughness of our sampling and that of Sprules (1975a) is that we detected 25 limnetic, macrozooplankton species in 20 lakes whereas Sprules found 28 species in 47 lakes. Seven of the species Sprules found were in only one or two lakes, and by sampling half as many lakes we would expect to find slightly fewer species.

Although our lower rate of loss of species is not likely due to thoroughness of sampling, the difference may well be due to lake size. Over 60% of Sprules' lakes were larger than our largest lake, and we both found lake size to be positively correlated with species diversity. However, this factor does not explain why our samples show that zooplankton communities in the La Cloche Mountain region do not show a drop in diversity until pH is at or below 5.5.

The following summary of species distribution is based on those species that occurred in 4 (20%) or more of the lakes we sampled. Species that occurred over almost the entire range of pH were *Mesocyclops edax*, *Diaptomus minutus*, *Polyphemus pedicularis*, *Holopedium gibberum*, *Diaphanosoma leuchtenbergianum*, and *Chaoborus* sp. Species restricted to a pH above 5 were *Epischura lacustris*, *Daphnia catawba*, and *Bosmina coregoni* and *B. longirostris*. Surveys of species distribution were cited earlier. Generalities supported by our study and these previous studies include the following. There is a universally observed reduction in species diversity as pH decreases. *Daphnia* are virtually absent below pH 5. Cyclopoids occur rarely below pH 5. Only one cyclopoid, *M. edax*, was found in one of our four lakes with a pH below 5. *Cyclops vernalis* may occur in a brief, spring pulse (Yan and Strus 1980), and this and other pulsatile species could be missed (DeCosta and Janicki 1978) by midsummer sampling such as ours. The macrozooplankton in northeastern, North American lakes with low pH are often numerically dominated by small species: usually *Diaptomus minutus* and *Bosmina* spp, but occasionally *Chydorus sphaericus* and *Cyclops vernalis* (Yan and Strus 1980). Our low pH lakes did not have *Bosmina*, but three of four were dominated by *Diaptomus minutus*. Yan and Strus (1980) found that *Diaptomus minutus* was absent from acidic, metal-contaminated lakes near Sudbury, Ont., but these lakes were dominated by *B. longirostris*. Only one of our acidic lakes, Cone Pond in New Hampshire, was dominated by moderately large zooplankton species; *Diaphanasoma leuchtenbergianum* and *Diaptomus spatulocrenatus*.

In contrast to northeastern North American lakes, Henrikson et al. (1980) and Eriksson et al. (1980) report that in Scandinavia, acidification produced a zooplankton community dominated by larger zooplankton. This difference can partially be attributed to an increase in larger copepod species in Scandinavia lakes (Eriksson et al. 1980), whereas the well-named *Diaptomus minutus* increases in North America.

The 1965 survey of 36 Adirondack Mountain lakes by Hall and Waterman (1968) is the only known published survey listing species of zooplankton for either the White Mountains or the Adirondack Mountains. Hall and Waterman sampled an unknown volume of Avalanche and Jones Lake in June and October of 1965 using an oblique tow, whereas we sampled a smaller, but known volume in July and August of 1979. Thus, some differences between our results could be due to techniques. For Avalanche Lake we did not find *Cyclops vernalis*, *Macrocyclops albidus*, *Eucyclops speratus*, *Poly-*

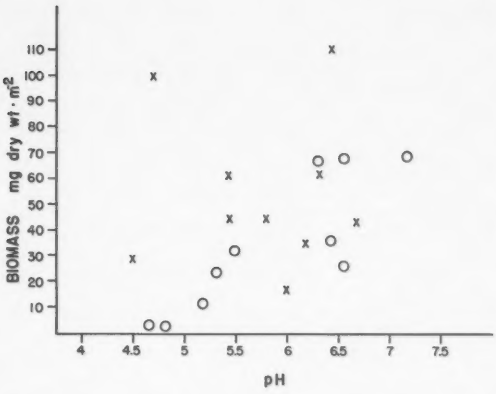

FIG. 2. The relation between pH and areal biomass estimates for the deepest part of each lake. Lakes from the Adirondack Mountains are represented by (o) and lakes from the White Mountains are represented by (x).

phemus or any *Daphnia* as reported by Hall and Waterman. We found only *Diaptomus minutus*, *Bosmina* sp., and *Chaoborus*. Hall and Waterman also detected *Diaptomus minutus*, but did not detect *Bosmina* and ignored *Chaoborus*. In Jones Lake, Hall and Waterman found that *Holopedium* and *Daphnia catawba* were "exceptionally abundant," *Diaptomus minutus* was abundant, and *Daphnia pulex* and *Diaphanasoma leuchtenbergianum* were present. Of these five species we detected only *Diaptomus minutus*. We did detect *Polyphemus* as fairly common and *Chydorus sphaericus*, *Alona rectangula*, and one specimen of a cyclopoid (unidentifiable). In contrast to our results, the presence in 1965 in Jones Lake of two species of *Daphnia* is highly indicative that the pH was higher 15 yr ago than the current pH of 4.7.

We found *Diaptomus spatulocrenatus* in three White Mountain lakes with a wide range of pH, but this species was not found in any of the 44 Adirondack lakes surveyed by Hall and Waterman and by us.

We show in Fig. 2 the relationship between zooplankton biomass and pH. Much of the scatter is due to two New Hampshire lakes, Black and Cone ponds. These two lakes appear to be quite different from each other (Appendix A) except that both are small, but biomass is not significantly correlated with area (see below). We determined stepwise and simultaneous, multiple regressions of biomass with all the variables listed in Table 1. Further, we tried a multiple regression omitting species number from the variables because the strong multicolinearity of pH and species number could obscure all statistical relationships to biomass. Neither simultaneous regression showed any significant relationship for biomass, perhaps because of multicolinearity among the independent variables. The stepwise regression showed that biomass was correlated with longitude and pH. Biomass showed a significant correlation with pH only after latitude or latitude and area were included in the stepwise, multiple regression (Table 2) even though biomass was not related to either of these latter two variables.

TABLE 2. Stepwise, multiple regression relating biomass (mg dry $wt \cdot m^{-2}$) over the deepest part of the lake to four variables. (*$P < 0.05$, df = 1,15.)

	Biomass	SE of biomass	F ratio
Longitude	−10.1	4.95	4.85*
pH	20.4	9.16	4.97*
Latitude	−36.6	30.4	1.45
Area (ha)	1.93	1.90	1.03
Regression constant = 120			
Regression $R^2 = 0.410$			
Regression standard error = 25.3			

The two extreme lakes distort a relationship between biomass and pH among the other 18 lakes. Omitting Black and Cone ponds, we determined stepwise and multiple regressions of biomass with the same variables as above. Biomass was not significantly related to any variable when species number was included in the simultaneous regression. However, biomass was significantly correlated with pH, and only pH, in the simultaneous regression when species number was omitted. Further, biomass was significantly correlated with pH, and only pH, in each of the stepwise regressions as each of the independent variables was added. In the simultaneous, multiple regression the F ratio for pH was 9.90 ($P < 0.01$, df = 1,10) with a slope and standard error of 22.6 and 7.2 mg dry $wt \cdot m^{-2}$, respectively. Over our observed pH range of 4.5−7.2, this regression predicts a change of 63 mg due to pH. The observed range for the 18 lakes is 64 mg. Among the 18 lakes pH appears as a very strong correlate of biomass.

Our results suggest a continual change in biomass over the entire range of pH even when all 20 lakes are considered. This relationship is clearer when only 18 lakes are considered. Other biomass studies have not shown as distinct a relationship. Yan and Strus (1980) found a difference in zooplankton biomass when an acid lake was compared to nonacidic lakes. However, they did not detect a continuous change in biomass with pH as there was no biomass correlation with pH among the several acidic lakes or among the several nonacidic lakes.

Discussion

Acidified, depauperate Scandinavian lakes have an increase in the mean length of the zooplankton community (Eriksson et al. 1980; Henrikson et al. 1980). This change has been interpreted as a response to a decrease in predation on large zooplankton species due to the loss of planktivorous fish and an increase in predation of small zooplankton by some invertebrate predators that were formerly kept in check by the fish. This response may be due to the prevalence of large copepods (Eriksson et al. 1980), especially *Heterocope saliens* Lill. (Raddum et al. 1980) in acidified lakes in Scandinavia. In contrast, acidified lakes of northeastern North America become dominated by small species partly because we lack a widely distributed, large copepod which is adapted to high acidity. The presence of the moderately large *Diaptomus spatulocrenatus* in the acidified Cone Pond of our

study is an interesting anomaly. Some acidified lakes show a relative increase or even the first appearance of moderate-sized zooplankton such as *Polyphemus*, *Holopedium*, or *Diaphanasoma*, but this size increase is counterbalanced by the loss of *Daphnia*. Normally *Diaptomus minutus* and/or *Bosmina* become predominant in acidified lakes of northeastern North America.

DeCosta and Janicki (1978) observed that *Bosmina* dominated some acidified waters in West Virginia. The duration of dominance of this small zooplankter was greater in acidified waters than in nearby nonacidic waters. They attributed the greater duration of dominance by *Bosmina* to the low tolerance of acidity by *M. edax* and its reduced abundance and predation on small prey in the acidic waters. On the other hand Eriksson et al. (1980) suggested that an increase in other kinds of invertebrate predators in acidified lakes, which also select for small prey, helps explain an increased mean size of zooplankton in acidified waters. Changes in the mean length of zooplankton communities in lakes undergoing acidification do not follow one consistent pattern, but seem to depend on preadaptations among the local, endemic fauna.

Numerous studies have now established that the zooplankton communities of thousands of lakes have been impoverished recently in association with the recent occurrence of acid rain. Many studies have established the link between acid rain and industrial emissions (for a review, see Haines 1981). Detailed studies that establish the proximate factor reducing zooplankton numbers are extremely difficult. Associated with acid rain are varying concentrations of metals from atmospheric deposition and local leaching, changes in the amount and species composition of available algae, reductions of planktivorous fish, and changes in invertebrate predators. Across the northern hemisphere the softwater lakes endangered by acid rain experience many combinations of the above variables. The proximate factor reducing zooplankton could be synergistic, and interpretation is complicated further by various preadaptations of isolated species or interspecies gene pools. None of these complications, however, obscure the clear relationship between industrial pollution of the atmosphere as the ultimate factor and the destruction of lake faunal systems.

Acknowledgments

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ALMER, D., W. DICKSON, C. EDSTROM, E. HORNSTROM, AND U. MILLER. 1974. Effects of acidification of Swedish lakes. Ambio 3: 330–336.

BURNS, C. W. 1969. Relation between filtering rate, temperature, and body size in four species of *Daphnia*. Limnol. Oceanogr. 17: 693–700.

CARTER, J. C. H. 1971. Distribution and abundance of planktonic Crustacea in ponds near Georgian Bay (Ontario, Canada) in relation to hydrography and water chemistry. Arch. Hydrobiol. 68: 204–231.

CRISMAN, T. L., R. L. SCHULZE, P. L. BREZONIK, AND S. A. BLOOM. 1980. Acid precipitation: the biotic response in Florida lakes, p. 296–297. *In* D. Drabløs and A. Tollan [ed.] Proc., Int. Conf. Ecol. Impact Acid Precipitation. Acid precipitation-effects on forests and fish project, Asa, Norway.

DECOSTA, J., AND A. JANICKI. 1978. Population dynamics and age structure of *Bosmina longirostris* in an acid water impoundment. Verh. Int. Verein. Limnol. 20: 2479–2483.

DEEVEY, E. S. JR., AND G. B. DEEVEY. 1971. The American species of *Eubosmina* Seligo (Crustacea, Cladocera). Limnol. Oceanogr. 16: 201–218.

ERIKSSON, M. O. G., L. HENRIKSON, B. I. NILSSON, G. NYMAN, H. G. OSCARSON, AND A. E. STENSON. 1980. Predator–prey relations important for the biotic changes in acidified lakes. Ambio 9: 248–249.

FRYER, G. 1980. Acidity and species diversity in freshwater crustacean faunas. Freshw. Biol. 10: 41–45.

HAINES, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. Trans. Am. Fish. Soc. 110: 669–707.

HALL, D. J., AND G. G. WATERMAN. 1968. Zooplankton of the Adirondacks. N.Y. Fish Game J. 15: 186–190.

HENDREY, G. R., AND R. F. WRIGHT. 1975. Acid precipitation in Norway: effects on aquatic fauna. J. Great Lakes Res. 2(Suppl.): 192–207.

HENRIKSON, L., H. G. OSCARSON, AND J. A. E. STENSON. 1980. Does the change of predator system contribute to the biotic development in acidified lakes? p. 316. *In* D. Drabløs and A. Tollan [ed.] Proc., Int. Conf. Ecol. Impact Acid Precipitation. Acid precipitation-effects on forests and fish project, Asa, Norway.

HOOVER, E. E. [ed.]. 1938. Biological survey of the Merrimack Watershed. N.H. Fish Game Dep. Surv. Rep. 3, Concord, NH.

LIKENS, G. E., AND J. J. GILBERT. 1970. Notes on quantitative sampling of neutral populations of planktonic rotifers. Limnol. Oceanogr. 15: 816–820.

MAKAREWICZ, J. C., AND G. E. LIKENS. 1975. Niche analysis of a zooplankton community. Science 190: 1000–1003.

NEWELL, A. E. [ed.]. 1963. Biological survey of the lakes and ponds in Sullivan, Merrimack, Belknap and Strafford counties. N.H. Fish Game Dep. Surv. Rep. 8B, Concord, NH.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. Statistical package for the Social Sciences, 2nd ed. McGraw-Hill, New York, NY.

PFEIFFER, M. H., AND P. J. FESTA. 1980. Acidity status of lakes in the Adirondack region of New York in relation to fish resources. NY State Dep. Environ. Conservation, Tech. Bull. FW-P168. Albany, NY.

RADDUM, G. G., A. HOBAEK, E. R. LOMSLAND, AND T. JOHNSEN. 1980. Phytoplankton and zooplankton in acidified lakes in south Norway, p. 332–333. *In* D. Drabløs and A. Tollan [ed.] Proc., Int. Conf. Ecol. Impact Acid Precipitation. Acid precipitation-effects on forest and fish project, Asa, Norway.

ROFF, J. C., AND R. E. KWIATKOWSKI. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55: 899–911.

SCHOFIELD, C. L. 1976. Acid precipitation: effects on fish. Ambio 5: 228–230.

SHANNON, C. D., AND W. WEAVER. 1949. The mathematical theory of communication. University of Illinois Press, Urbana, IL.

SPRULES, W. G. 1975a. Midsummer crustacean zooplankton communities in acid-stressed lakes. J. Fish. Res. Board Can. 32: 389–395.

1975b. Factors affecting the structure of limnetic crustacean zooplankton communities in central Ontario Lakes. Verh. Int. Verein. Limnol. 19: 635–643.

YAN, N. D., AND R. STRUS. 1980. Crustacean zooplankton communities of acidic, metal-contaminated lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 37: 2282–2293.

Appendix A

Physical and biological parameters of surveyed lakes including those used in regression analyses.

Lake	State	Longitude	Latitude	Elevation (m)	Area (ha)	pH (late summer values) 1938[b] or 1939	pH (late summer values) 1950,[c] 1951, or 1952	pH (late summer values) 1970s[d]	Species[e] no.	All[f]	Secchi (m)	Depths[g]	Maximum depth (m)	Biomass[h]
Jones Lake	NY	74°38′	43°21′	698	6.3	—	—	4.7	3	6	5.0	4	4.3	4.5
Avalanche Lake	NY	73°53′	44° 7′	872	3.2	—	—	4.8	3	3	4.5	4	7.5	4.1
Thirsty Pond	NY	74°54′	43°49′	647	11.3	—	—	5.2	3	5	2.8	3	3.0	10.4
Buck Pond	NY	74°53′	43°49′	614	7.6	—	—	5.3	6	6	5.0	4	8.1	24.1
Razorback Pond	NY	74°55′	43°50′	668	4.7	—	—	5.5	5	7	3.0	4	6.0	32.3
Second Pond	NY	74° 5′	43°39′	683	10.5	—	—	6.3	7	7	2.8	3	3.5	65.2
Heart Lake	NY	73°58′	44°10′	661	11.3	—	—	6.4	8	8	4.3	4	9.0	35.5
Round Lake	NY	73°54′	44°13′	635	18.9	—	—	6.6	9	9	3.8	3	3.5	25.5
Chatiemac Lake	NY	74° 2′	43°38′	698	12.6	—	—	6.6	8	8	1.0	4	7.5	67.5
Upper Cascade Lake	NY	73°52′	44°13′	620	10.4	—	—	7.2	10	10	8.5	4	10.0	68.1
Lake Constance[a]	NH	72°	44°	469	7.7	—	5.6	4.5	4	6	2.3	3	5.5	29.6
Cone Pond	NH	71°36′	43°54′	468	4.1	—	5.2	4.7	3	6	7.0	4	8.5	101
Upper Hall Lake	NH	71°33′	43°52′	484	10.1	6.2	5.4	5.4	8	8	3.3	4	11.5	62.7
Loon Pond	NH	71°38′	44° 2′	734	5.7	6.2	6.1	5.4	5	7	6.5	4	8.5	45.1
Russell Pond	NH	71°39′	44° 1′	504	9.0	6.6	—	5.8	6	7	12.3	5	23.7	45.2
Echo Lake	NH	71°41′	44°11′	599	8.1	6.9	—	6.0	7	8	6.0	4	11.9	17.0
Little Sawyer Lake	NH	72°23′	44° 3′	617	4.9	—	6.2	6.2	7	7	7.5	4	8.5	34.5
Wachipauka Lake	NH	72°55′	43°58′	455	8.9	6.7	6.4	6.3	6	7	3.2	4	8.0	61.9
Black Pond	NH	71°35′	44° 6′	503	4.1	—	6.2	6.4	7	8	4.3	4	12.7	111
Mirror Lake	NH	71°42′	43°56′	212	10.1	6.8	6.3	6.7	8	11	6.5	4	11.0	44.1

[a]Anaerobic hypolimnion.
[b]Values from Biological Survey of the Merrimack Watershed, No. 3, New Hampshire Fish and Game Department (1938).
[c]Values from Biological Survey of the Lakes and Ponds in Sullivan, Merrimack, Belknap, and Strafford Counties, New Hampshire Fish and Game Department (1963).
[d]New Hampshire lakes sampled at 1 m, July 1979. New York data from C. Schofield (personal communication), sampled just below surface, June 1975.
[e]Number of species whose numerical abundance exceeds 0.1% of all individuals in sample.
[f]Number of all detected species.
[g]Number of depths sampled.
[h]Biomass estimates in g dry wt·m^{-2} over deepest part of lake: average of an early July and an early August set of samples.

Appendix B

Species whose numerical abundance exceeds 0.1% of all individuals are indicated by X. Species that were detected but were rarer are indicated by O.

	Lake Constance, NH	Cone Pond, NH	Jones Lake, NY	Avalanche Lake, NY	Thirsty Pond, NY	Buck Pond, NY	Upper Hall Lake, NH	Loon Pond, NH	Razorback Pond, NY	Russell Pond, NH	Echo Lake, NH	Little Sawyer Lake, NH	Wachipauka Lake, NH	Second Pond, NY	Heart Lake, NY	Black Pond, NH	Round Lake, NY	Chatiemac Lake, NY	Mirror Lake, NH	Upper Cascade Lake, NY
Epischura lacustris (Forbes)						X					X						X	X	X	X
Diaptomus sanguineus (Forbes)																				X
D. minutus (Lill.)	X		X	X	X	X	X	X	X	X	X	X	X		X		X	X	X	X
D. spatulocrenatus (Pearse)		X					X									X				
D. leptopus (Forbes)								X												
D. oregonensis (Lill.)														X						
Tropocyclops prasinus (Fischer)						X											X			X
Cyclops scutifer (Sars)							X	X										X	X	X
Mesocyclops edax (Forbes)	X						X		X		X	X	X	X	X	X	X		X	
Eucyclops agilis (Koch)		O																		
Cyclops sp.			O		O															
Daphnia dubia (Herrick)																				X
D. catawba (Coker)						X			X	X	X	X	X		X	X	X	X	X	
D. ambigua (Scourfield)	O						X									X		X		
D. galeata (Sars)															X					
Daphnia sp.					O			O						X					O	
Bosmina coregoni (Baird)	X									X	X	X			X	X		X		X
B. longirostris (Müller)					X	X	X	X	X				X	X			X		X	
Bosmina sp.				X																
Alona rectangula (Sars)			O																	
A. quadrangularis (Müller)		X																		
Leptodora kindtii (Lill.)														X			X			
Sida crystallina (Müller)																				X
Polyphemus pediculas L.			X		X				O	X	O					O			O	X
Latona setifera (Müller)											X									
Diaphansoma leuchtenbergianum (Lieven)		X								X		X		X	X	X	X	X		
Holopedium gibberum (Zaddach)	O	O				X	X	O	X	X	X	X	X	X	X		X	X	X	X
Chaoborus	X	O	X	X			X	X	O	O		X	X			X			X	
Chydorus sphaericus (Müeller)			O																	

Production Modeling Using Mortality Estimates

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CSIRKE, J., AND J. F. CADDY. 1983. Production modeling using mortality estimates. Can. J. Fish. Aquat. Sci. 40: 43–51.

Two new approaches to applying the logistic model to fisheries data are suggested; these do not employ information on fishing effort, but use the overall mortality rate (Z) for the population as a direct index of fishing mortality rate (F). The first approach suggests fitting a parabola between annual yield and mean annual Z, and provides an independent estimate of natural mortality M; the second suggests fitting a straight line directly between catch rate and mean annual Z. Both approaches use data sources that are statistically independent and encourage a smooth transition from an early use of production models in a developing fishery into the use of more elaborate analytical models as the data base accumulates.

Key words: Theory of production modeling, logistic population growth, use of mortality parameters in fitting

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On propose deux nouvelles méthodes pour l'application du modèle logistique aux données de la pêche, qui n'utilisent pas les données sur l'effort de pêche, mais le coefficient de mortalité totale (Z) comme indice direct du coefficient de mortalité due à la pêche (F). Avec la première méthode, on ajuste une parabole en fonction du rendement annuel et de la moyenne annuelle de Z pour obtenir une estimation indépendante de la mortalité naturelle M. Avec la seconde, on ajuste une droite à la relation entre le taux de capture et la moyenne annuelle de Z. Les deux méthodes conduisent à l'utilisation de données statistiquement indépendantes et favorisent un passage facile des modèles initiaux de production pour une pêche en développement aux modèles analytiques plus élaborés, au fur et à mesure qu'augmente la base des données disponibles.

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PRODUCTION models are among the simplest and most widely used approaches in the assessment of exploited fish populations. They originated with Graham (1935), who provided a simple formulation to relate the instantaneous rate of surplus production of a fish population to its current biomass and to the difference between the actual biomass and the carrying capacity or maximum biomass the environment will support. Later on Schaefer (1954) introduced a method of estimating the surplus (harvestable) production of a fish population for each year by relating the changes in abundance or catch rate to the total fishing effort; a measure which is intended to be directly proportional to the fishing mortality rate (F) exerted on the population. Because of the ease of application of these models in their simplest form, the collection of catch and effort statistics, and their subsequent utilization in production models has become the standard approach to fisheries assessment in many parts of the world.

Despite recent and sophisticated advances in multicomponent (e.g. ecosystem) modeling, production models "will continue for some time to serve as a basis for management of many of the world's fisheries" (Uhler 1979). In particular, stock assessments for those fisheries lying outside the jurisdiction of the "developed" countries will still have to rely on simple, robust methods that require easy-to-obtain data, and that can be used by field biologists with "hands-on" experience of the fisheries in question, but who may lack advanced training in population dynamics and who do not necessarily have access to sophisticated computing equipment. In these real-world situations, it should be stressed that the conclusions based on the application of any particular model must be compared with all other available information to be sure that anomalous fits or erroneous data are, wherever possible, revealed, and that this information is used in a feedback loop to decide on interpretation of results and on future management policies (Ludwig 1981). From this point of view, the objective of the authors has been to produce an extension of a well-known method which will be useful in permitting production models to be developed for use in conjunction with annual estimates of overall mortality, Z; one of the first and simplest variables that can be obtained from an analysis of

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size and age composition characteristics of the population under study.

Nowadays, the fisheries literature is quite rich in both successful and not so successful examples of the use of surplus production models, including developments introduced by Pella and Tomlinson (1969), Fox (1970), and more recently, Schnute (1977). In general, the sometimes uncritical application of these types of models depends only on the availability of sets of annual data on total catch and total fishing effort. Information on total catch or annual yield is comparatively simple to obtain, and normally is the first type of data to be collected when a fishery statistical system is established. The same does not apply to fishing effort data which, for assessment purposes, have to be expressed in standardized units to account for differences in size and type of vessels and fishing gear being used, and are affected by changes in the degree of aggregation of both the resources and the fleet (Rothschild and Robson 1972), all of which factors affect (q), the overall catchability coefficient. Moreover, history has shown that as a fishery develops there is a regular need to introduce corrections to the nominal fishing effort to account for changes in efficiency, learning, fishing pattern, and strategy, etc., which change from year to year; not to mention the possible changes in the distribution, behavior, and species composition of the fishable stocks. All this may affect the catchability coefficient and therefore affect the value of each unit of effort, with the consequence that the basic assumption that fishing effort (f) is proportional to F will no longer remain valid. Unfortunately, these changes are impossible to assess without independent data on mortality rates, and are difficult to detect in time to be incorporated in an assessment, particularly for developing fisheries. Needless to say, a lack of proper fishing power calibration can lead to misleading results when stock assessment techniques rely almost entirely on the availability of fishing effort data, and can particularly (but not exclusively) prove to occur in the earlier years of a newly developed fishery when the learning curve of the fishermen is particularly steep (Brown et al. 1976).

Two other problems also present difficulties in defining the true fishing effort. These may occur, for example, in some tropical fisheries where there is a variable mixture of species all exploited by the same fleet. In this case it may be impossible to estimate how much effort is being directed into the exploitation of a given species. In other cases, the existence of a very heterogenous and changeable fleet may also prevent the definition of suitable units of effort. Therefore reliable indices of abundance or catch rates for the overall fleet may not be available, particularly if effort units are not available for all components fishing, for example, a stock shared by more than one country. All of these factors result in sharp reduction of usable stock assessment methods simply because of problems in effort definition.

In this paper we propose a new approach that may allow fitting of surplus production models in the absence of effort data. However, it should be noted that the proposed methods do rely on the same assumptions as the Graham (1935) and Schaefer (1954) models, and share most of the limitations of such a simplistic relationship beween indices of mortality and total yield used in other production models, for details on which we refer to the authors mentioned above. At the same time, this approach has several important advantages in certain instances over the usual estimation procedure based on catch and effort data.

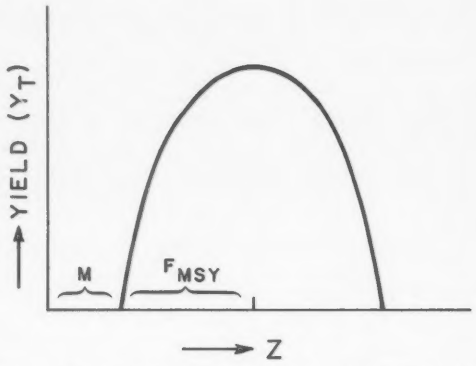

FIG. 1. Relationship between Y and Z when population growth follows a logistic curve.

Instead of looking at the relationship between total annual yield (Y) and total fishing effort (f), compare instead Y against an overall estimate of the total mortality coefficient (Z) for a given stock over a series of years. We might then expect the production curve to look like Fig. 1 where the value of Z can be split into its two components: the natural mortality coefficient (M) to the left, and the fishing mortality coefficient (F) to the right of where the left-hand side of the surplus production parabola intercepts the abscissa.

If we had a series of values of Z (possible from biological samples) and Y, this would allow the production curve to be fitted directly in the absence of effort data, thus avoiding the problems of having to estimate total standardized effort and having to correct for changes in fishing power and fishing pattern, increased efficiency, learning, etc. It also suggests an alternative method of estimating M and hence F. Also, because this method begins to combine the previously separated analytical and surplus production model approaches, it leads naturally into the greater use of analytical techniques, allowing for a more detailed analysis of developing fisheries.

A second variant of this approach is also suggested for situations where neither total catch nor effort data are available, but only an annual index of total mortality rate (e.g. mean size) and catch rate (U), both of which are sample statistics which may be available from research survey data or limited sampling of the commercial fleet. Although this second approach does not allow estimation of maximum sustainable yield (MSY) directly, it does allow estimation of the position of the fishery relative to F_{MSY}, as well as the general shape of the yield curve, which may be particularly useful in preliminary assessments.

Theory

Two main approaches to the use of production modeling with mortality data seem possible, depending on the kind of basic data available: (a) if total catch and Z are known for a

series of years, (b) if catch rates and Z are known for a series of years.

In neither case is a direct knowledge of the effort level needed. We can obtain independent estimates of Z from tagging experiments, from catch curve analysis, from data on mean length, etc. In addition, data on either the total catch from the stock, or some index of the annual abundance of the stock is needed. In this latter case, we may use mean catch rate (U), or if mean biomass estimates per unit area are available (e.g. from trawl surveys or acoustic surveys), these can be used directly in a regression against Z. This approach can prove to be useful even if, as for a number of tropical fisheries, neither total catch nor total effort are known, as long as some annual indices of total mortality (Z) and of abundance (U) are available. The basic theory behind these approaches is as follows.

When Estimates of Total Annual Catch and Z are Available for a Series of Years

In this case we may want to go back to the logistic model of population growth proposed by Graham (1935), (see Ricker 1975), where equilibrium yield (Y_E) is:

$$(1) \quad Y_E = \frac{r\bar{B}(B_\infty - \bar{B})}{B_\infty}$$

where, $\bar{B}$ = average biomass
B_∞ = size of the virgin population or carrying capacity of the environment, assumed to be a constant.
r = net specific rate of increase of the population when growth-limiting factors are removed. r is also assumed to be constant and a characteristic of the given stock.

To express the equilibrium yield equation (1) in terms of the fishing mortality coefficient (F), we divide both sides of the yield equations by $\bar{B}$, so that:

$$\frac{Y_E}{\bar{B}} = \frac{r}{B_\infty}(B_\infty - \bar{B}) = F_E$$

(because at equilibrium, $Y_E = F_E\bar{B}$)

solve for $\bar{B}$, where

$$\bar{B} = \frac{(r - F_E)}{r} B_\infty.$$

Then replace $\bar{B}$, and the yield equation (1) above becomes:

$$Y_E = B_\infty F - B_\infty \frac{F^2}{r}.$$

We then replace F (where $F = Z - M$):

$$Y_E = B_\infty(Z - M) - B_\infty \frac{(Z^2 - 2ZM + M^2)}{r}$$

which expands to:

$$Y_E = -\left(B_\infty M + B_\infty \frac{M^2}{r}\right) + \left(B_\infty + 2B_\infty \frac{M}{r}\right) Z - \left(\frac{B_\infty}{r}\right) Z^2.$$

Because under ideal equilibrium conditions we can assume that all terms within parentheses are constant, we can reduce the equation above to a quadratic equation of the form:

$$(2) \quad Y = c + bZ + aZ^2.$$

This corresponds to a parabola with a "convex-downwards" curvature as in Fig. 1, where:

$$a = -B_\infty / r$$

$$b = B_\infty\left(\frac{r + 2M}{r}\right)$$

$$c = -B_\infty\left(\frac{rM + M^2}{r}\right).$$

We know that when $F = 0$, $Y = 0$, and $Z = M$, equation (2) becomes:

$$Y_E = c + bM + aM^2 = 0 \text{ (when } F = 0)$$

and we can now solve for natural mortality, where:

$$M = \frac{-b + \sqrt{(b^2 - 4ac)}}{2a}.$$

We can also solve for Z (Z_{MSY}) giving the maximum equilibrium or MSY, which occurs when:

$$\frac{dY}{dZ} = \frac{d}{dZ}(c + bZ + aZ^2) = 0.$$

Then,

$$\frac{dY}{dZ} = b + 2aZ = 0$$

$$Z_{MSY} = -\frac{b}{2a}.$$

When expressed in terms of the parameters of this revised logistic model, Z_{MSY} becomes:

$$Z_{MSY} = 0.5r + M$$

and in terms of the fishing mortality F, giving the MSY, is:

$$F_{MSY} = Z_{MSY} - M.$$

Another important relationship is:

$$F_{MSY} = 0.5r$$

or the net specific rate of increase in population biomass is:

$$(2a) \quad r = 2F_{MSY}.$$

Maximum sustainable yield can then be found by replacing Z_{MSY} in the quadratic equation (2) above, so that:

$$MSY = c + bZ_{MSY} + aZ_{MSY}^2$$

or alternatively,

$$MSY = c - \frac{b^2}{4a}.$$

If we express the MSY in terms of the parameters of the logistic model, it becomes:

$$\text{MSY} = -\frac{B_\infty(rM + M^2)}{r} + \frac{(B_\infty r + 2MB_\infty)^2}{4B_\infty r}$$

$$= \frac{B_\infty r}{4}.$$

As this also gives:

$$B_\infty = \frac{4(\text{MSY})}{r}$$

$$B_\infty^2 = 4(\text{MSY})\frac{B_\infty}{r},$$

then:

$$B_\infty = \sqrt{4(\text{MSY})\,(-a)};\ (\text{where, } a = -\frac{B_\infty}{r})$$

and:

$$r = -\frac{B_\infty}{a}.$$

When Estimates of Catch Rate and Z are Available for a Series of Years

It is often useful in the early stages of the assessment of a stock, or when an overall estimate of total landings or effort are not yet available (e.g. for a shared resource where only data from one country fishing the common stock is available), to carry out a preliminary analysis to determine where the fishery is in relation to some (as yet unknown) MSY condition. The following approach may then be worthwhile:

Assume the Schaefer (1954) model[1] where:

$$U_t = U_\infty - bt_t.$$

Replace f (where $f = F/q$):

$$U_t = U_\infty - b'F_t \text{ (where } b' = b/q).$$

Then replace F above (where $F = Z - M$):

$$U_t = U_\infty - b'(Z - M)_t = U_\infty - b'Z_t + b'M$$

$$U_t = (U_\infty + b'M) - (b')Z_t$$

... i.e. the model is expressed in terms of catch rate, without necessarily implying that either total catch or statistics of total effort are available.

If the equilibrium conditions assumed in the original production model are satisfied, then the values within parentheses above are both constant, thus making it possible to fit a (functional) regression of the form:

$$y = A - Bx$$

where

$$B = \hat{b}' = q\frac{B_\infty}{r}$$

and

$$A = U_\infty + b'M = q\frac{B_\infty}{r}(r + M).$$

In some cases the mean catch rate of the virgin stock (U_∞) can be approximated by the catch rates obtained by a standard (research or commercial) vessel or class of vessel, during the first years of the fishery, then:

$$F_{\text{MSY}} = \frac{U_\infty}{2b'} \quad \text{from eq (2a)}$$

$$\hat{M} = \frac{A - U_\infty}{B}$$

and

$$r = \frac{A}{B} - \hat{M}.$$

An alternative way of solving can be to obtain an independent estimation of M[2] which, together with the values of A and B obtained from the regression above, allows the estimation of:

$$r = \frac{A}{B} - \hat{M}$$

and

$$F_{\text{MSY}} = 0.5r.$$

It will not be possible to obtain an absolute value of B_∞ or MSY through this approach, but some idea of the shape of the yield curve can be obtained, together with an estimation of where the fishery is in relation to MSY conditions.

Beside the MSY bench mark, one other criterion of optimality that can be derived from parallel series of Z values and catch rates even without estimates of M and U_∞ is the yield at Maximum Biological Production (Y_{MBP}), which corresponds to the total production being harvested as well as being removed by natural mortalities. A biological production curve can be obtained empirically by multiplying our regression equation by different values of Z along the abscissa and plotting (Fig. 2), i.e. our index of biological production is: $U_tZ_t = (U_\infty + b'M)\,Z_t - b'Z_t^2$, which describes a parabola. By differentiation, this gives a maximum at:

$$\frac{d(U_tZ_t)}{dZ} = (U_\infty + b'M)\,Z - b'Z^2 = 0$$

$$= A - 2b'Z = 0$$

---

[1]The Graham equation is easily transformed into that used by Schaefer (1954), i.e., when expressing Y_F in terms of F, equation (1) becomes:

$$Y_F = B_\infty F - \frac{B_\infty}{r}F^2.$$

Divide by f so that:

$$U = \frac{Y}{f} = \frac{B_\infty}{f}F - \frac{B_\infty}{rf}F^2 = qB_\infty - \frac{q^2B_\infty}{r}f$$

where: $f = F/q$; $U_\infty = qB_\infty$; $b = q^2\frac{B_\infty}{r}$; therefore: $U_t = U_\infty - bf_t$; the conventional Schaefer formulation.

[2]An estimate of M may be obtained, for example, by the method of Pauly (1980); or a value of M for stocks of the same species found elsewhere (e.g. from the compilation in Beverton and Holt 1959) may be used as a first approximation.

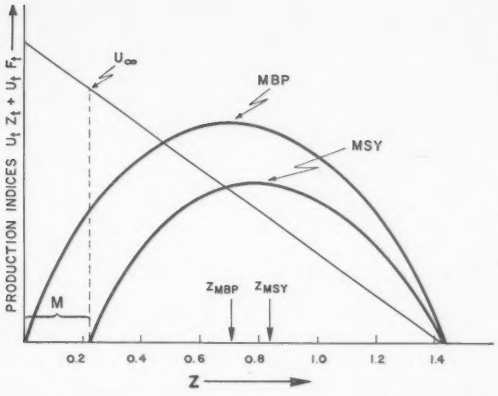

FIG. 2. Relationship between the catch rates and total mortality coefficients (straight line) and production curves. Yield curve is expressed as a function of U_iF_i over Z_i and biological production curve is expressed as a function of U_iZ_i over Z_i.

i.e.

$$Z_{MBP} = \frac{A}{2b'}$$

$$= 0.5(r + M)$$

thus implying that F_{MBP} occurs at a level below the F_{MSY}. Further implications of this criterion are explored in Caddy and Csirke (unpublished data).

Data Base and Applications

Total catch is undoubtedly the first statistic needed in a fishery, and especially for a newly developed one will require the main efforts of the fisheries departments to collect the necessary data, either by a stratified sampling survey (Gulland 1966; Bazigos 1974) or by complete census. Adding the further requirements for collection of effort data, entailing a logbook or port interview system, and the subsequent calibration and summarization of fishing effort for a variety of boats and gears, poses still further strains on the fisheries departments, especially for developing countries. If and when the further necessary transition to analytical models is proposed, involving yet another sampling survey of landed catch for size or age composition (allowing for more detailed predictions of effects of size limits and quotas), this can usually be achieved only by less effort (and hence less precision) directed to the two previous survey methodologies. As a result, many countries are now 'stuck' at the level of production model analysis without possibility of inaugurating sampling schemes for size and age from the catch, and even if the transition from production to analytical model occurs, this normally causes a gap due to the existing differences in two types of analysis.

The first approach suggested here, in addition to giving an estimate of M and largely avoiding biases due to incorrect effort calibration, has the major advantage that, instead of perpetuating the present division between the two main schools of analysis, it leads naturally into use of analytical models, or methods such as those of Pauly (1980), Paloheimo (1980), Deriso (1980), Evans (1981), and Shepherd (1982), which combine effort data with the use of analytical parameters.

Estimation of Total Yield

A reliable estimation of the total annual catches is required, as in most stock assessment methods, for the application of the first method suggested above. There are, however, some potential sources of errors regarding the application of this method that need to be underlined. One requirement of the data is that catches and accompanying Z values in the early years of the fishery are well known. If these are missing, the resulting estimate of M will be poor. Non-reporting of sections of the catch (e.g. discards) will also lead to errors in the estimates (especially overestimates of M).

Estimation of Catch Rates

For the application of the second method, it is assumed that an annual estimate of abundance exists. This can be obtained by sampling fishing operations, or still better from surveys, or acoustic prospection. Also it should be possible to assume that the abundance estimate is integrated throughout the year, and that the catch rate represents abundance of a unit stock.

The obvious advantage of the catch rate versus Z plot is that in absence of total landings, it is still possible to fit a production model from variables easily derived from commonly available sample statistical data: namely, the catch rate (a particular standard vessel class can be used), and the overall mortality rate Z from stratified random samples of size frequencies from catches made by all types of gear (including discards!). For estimating total mortality, the methods summarized in Van Sickle (1977), Pauly (1980), and Jones (1981) seem particularly appropriate. Clearly, this approach may be quite efficient in terms of the total manpower needed.

In this case we also have some potential sources of errors. Other than those for the usual method of fitting (especially definition of the unit stock and catch rate calibration), the main problem is in definition of U_∞ in absence of the usual regression fit of catch rate (U) versus effort (f). It is suggested that a reasonable approximation can be based on the assumption that the true value of U_∞ is within the limits $U_1 < U_\infty < U_x$, where U_1 = catch rate in 1st year of the fishery, and $U_x = U_1 + \Delta U$; given that $\Delta U = U_1 - U_2$.

The tendency now in countries around the North Atlantic is to place more emphasis on development of direct estimates of fish abundance by research survey. This trend (which largely originated as a result of the imprecision of commercial estimates of abundance), favors the use of mortality data in population analysis, perhaps at the expense of expensive and imprecise methods of collection of fishing effort data (e.g. Clark 1979).

Estimation of Z

The application of the methods being proposed relies

mainly on the availability of estimates of Z for a series of years. Besides the possibility of using marking data [see Jones (1976) for general description of methods commonly used] to estimate rate of survival and therefore Z, there are a variety of methods for estimating Z by sampling commercial landings. These are found in the literature summarized, for example, in Gulland (1969), Pauly (1980), and Jones (1981).

What is not usually stated is that these estimates can be classified into those giving mean estimates ($\bar{Z}_t$) integrated over the past life span of all age-groups (or all fully recruited age-groups) present in the fishable population at time t, and those estimates (Z_t) which measure the current mortality rate for one or more year-classes over the period $t-1$, t.

The first category includes:

1) Estimates obtained by fitting a log-linear regression to the right-hand side of the catch curve (see Robson and Chapman 1961); this gives the Z for the fully recruited ages only.

2) Estimating Z from Jones (1981) cohort analysis. This requires knowledge of L_∞ and M/K, and can provide either an annual value of Z for all fully recruited age-groups, or Z for all age-groups fully or partially retained; weighted by abundance: i.e.:

$$\hat{Z} = \frac{\Sigma Z_l C_l}{\Sigma C_l}$$

where C is either catch in numbers or weight of size category l.

3) Methods that obtain Z as a function of mean size ($\bar{l}$), as proposed by Beverton and Holt (1956), to obtain a value of Z that is weighted to include all fully or partially retained age-groups, where:

$$\hat{Z} = \frac{K(L_\infty - \bar{l})}{\bar{l} - l_c}.$$

4) Ssentongo and Larkin (1973) propose an unbiased version of this equation where:

$$\hat{Z} = K\left(\frac{n}{n+1}\right)\left(\frac{1}{\bar{y} - y_c}\right)$$

where n = sample size;

$$\bar{y} = -\ln\left(1 - \frac{\bar{l}_t}{L_\infty}\right) \text{ and } y_c = -\ln\left(1 - \frac{l_c}{L_\infty}\right).$$

5) Pauly (1980) has also expressed this in terms of the mean weight $\bar{w}$ in the catch, where:

$$\hat{Z} = \frac{nK}{(n+1)\ln(A/B)}$$

and where

$$A = (3\sqrt{W_\infty} - 3\sqrt{W_c})$$

and

$$B = (3\sqrt{W_\infty} - 3\sqrt{\bar{W}}),$$

W_c being the weight at first capture, and W the asymptotic weight.

The second category includes:

1) Comparison of catch (or more likely, catch rates) at age j of a cohort in successive years:

$$Z = \ln\left(\frac{U_j}{U_j - 1}\right).$$

2) Modifications of the above method such as Heinke's method (Robson and Chapman 1961):

$$Z = \ln\left(\frac{\Sigma N - N_0}{\Sigma N}\right)$$

where N_0 is the number in the youngest, fully recruited age-group, and N is the sum of the number of individuals in all ages from N_0 upwards (Robson and Chapman 1961).

3) Cohort analysis (Gulland 1965; Pope 1972) which provides estimates of F provided M is known.

In general terms, this second type of annual estimate of Z_t is less valid for use in a production model than those for $\bar{Z}$, because a comparison of Z_t with annual yield Y_T for multi-age stocks has not been adjusted for departures from equilibrium conditions. This is not the case for values of $\bar{Z}$, which are based on an integral of the effects of all previous years' fishing and natural death rates on all age-groups still in the fishery. Ideally, to write an expression for the total biomass of deaths $D = B\bar{Z}$, the value of Z should be the weighted value for the whole population (partially or fully recruited). This, as indicated above, is given by either Beverton and Holt's method, or a weighted mean Z from length cohort analysis. Using Heinke's method or its more efficient subsequent derivations (Robson and Chapman 1961), or using catch curve analysis, gives an estimate of Z for fully recruited age-groups, which, strictly speaking, is an overestimate of $\bar{Z}$. What errors if any are introduced into the estimate of MSY by using Z's obtained in this fashion are not immediately obvious, but it is expected that the value of M obtained in this way may be too high. However, if Y_T is replaced by the yield of fully recruited ages only, this bias may be avoided. In any case, as long as the method of calculating Z is specified, and changes in the way that Z is calculated are not introduced into the time series, the fitting of the model should not be seriously affected.

In all cases a basic knowledge of either the age structure or of the growth parameters (K, the growth coefficient, and L_∞, the asymptotic length in the von Bertalanffy growth equation) is needed to get an estimation of Z (e.g. Van Sickle 1977; Jones 1981). However, it should be noted that even when the age structure and K are unknown, fitting a production model of the type proposed here is still possible provided Z/K can be estimated from size data. As pointed out to us by D. Pauly (International Center for Living Aquatic Resource Management MCC, P.O. Box 1501, Makati, Metro Manila, The Philippines, personal communication), this will allow fitting yield against Z/K, which will give an estimate of MSY as well as Z_{MSY}/K, F_{MSY}/K, M/K and the exploitation ratio (E), where $E = F/Z = 1 - (M/K)/(Z/K)$, which are useful estimates that can be then used in subsequent yield per recruit analysis. For this purpose estimates of Z/K can be derived using the Beverton and Holt (1956) equation if estimates of L_∞, l_c and average length are available, or by the method of determining Z/K by regressing the cumulative catch in number against size suggested by Jones (1981).

Estimating Biomass

Noting that $Z = M + F = M + \frac{Y_t}{B_t}$, we can estimate directly the biomass of the stock given the values for F and Y_t, as $B_t = Y_t/(-Z - M)$. This has considerable value, for example, by comparison with an annual estimate of recruitment, we can obtain an idea of the spawner–recruit relationship for the stock.

Equilibrium Approximation

If a value of Z is obtained from catch curve analysis or from mean size, this automatically incorporates mortality rates suffered in earlier years, although trends in recruitment and availability are possible sources of bias with this estimate of Z. In this respect Ricker (1975) notes that "Ordinary catch-curve methods... give estimates which tend to lag several years behind the time the data are collected, and which represent average conditions during the years of recruitment."

In the second method therefore, a plot of $\bar{Z}$ against U should more closely approximate equilibrium conditions than for the catch–effort approach.

In the first method, however, the catch in a given year does not strictly represent an equilibrium condition, as can be illustrated if F falls to zero in a given year, when Z will not fall to M instantaneously, if based on mean size or a catch curve: this would result in an anomalous point for $Y_T = O$ on the abscissa to the right of M.

The precise adjustment needed to allow for effects of non-equilibrium condition in effort models has been the subject of a number of papers (Schaefer 1954; Gulland 1961; Walter 1975), but more recent theory follows Schnute (1977) and Uhler (1980) in moving towards stochastic versions of the Graham–Schaefer model, using arithmetic mean values of effort in successive years, and arithmetic or geometric mean catch rates in successive years to compensate for departures from equilibrium.

In some ways, the use of statistically independent variables Z and Y should provide estimates that are more reliable than the ones obtained from a regression of c/f over f, although an exact estimate of the error term for the direct parabola fit needs further theoretical investigation because, as noted by J. Beddington (International Institute for Environment and Development, 10 Percy Street, London N.W., personal communication), the estimation, particularly of M, is subject to errors in direction parallel to both the X and Y axes. As noted by several authors (Uhler 1980), catch rate (or the catch–effort ratio) is a proxy variable, and its use in a regression equation with an autocorrelated variable, fishing effort, may result in biased estimates being obtained from regression procedures, hence requiring a more complex simulation approach for accurate parameter estimation. This appears not to be the case for either of the methods discussed here.

Approaches to Fitting the Model

It is not our intention in this communication to propose or justify one single 'best' method of fitting this model: this will require more experience with the model and more extensive work of the kind described by Hilborn (1979), which would probably be premature at this point. We believe further testing and discussion of different fitting procedures is needed, but we realize that this will go beyond the main objective of this paper. However, our experience to date with fitting the model to 'real' data has appeared to provide reasonable estimates of both MSY, F_{MSY}, and M, compatible with the results of other methods, although, as pointed out by one of the referees of an earlier draft of the paper, this does not constitute a definitive proof of the validity of the results obtained, as both methods could be equally biased. From preliminary results of testing this type of production model using a deterministic simulation with a self-regenerating age-structure, it was clear that there are multiple possibilities for pretreatment and actual fitting of the model. During this phase of preliminary testing, some problems and suggested procedures were revealed that are passed on for the information of possible users of the model, without in any way suggesting that these procedures are definitive. In general, we recommend caution in extracting management implications from the model at this stage, unless it is supported by the results of other analyses.

In addition to simply fitting by eye (which has appeared feasible in several cases because of the reduced 'noise' in the data compared with many production model fits with catch effort data), two main methods of estimating model parameters were tested. These methods were:

a) Direct fitting of a parabola to a series of annual values of yield (Y_t) and overall mortality ($\bar{Z}_t$) with or without prior application of standard techniques of equilibrium approximation to the data. In this approach, the second-order polynomial given in equation 2 is fitted by the least squares method directly, or through a multiple regression routine as if the variables Z_t and Z^2_t were independent. Although these methods give 'satisfactory' fits in many cases, care must be taken to check the fit graphically, as there is no guarantee that the parabola will be concave downwards (other fits should of course be rejected).

Theoretical objections to this method of fitting have been raised by J. Beddington (personal communication), who postulates that the estimates of M generated by this method are likely to be underestimates. This was confirmed by several simulations, although the degree of underestimation will, of course, depend on the smallest total mortality estimates in the series: if data are available from the early years of the fishery, when total catches and therefore F's are low, this in effect 'forces' the intercept to pass through the abscissa close to the true value of M. The estimates of M, even with the above possible bias, may still be useful, particularly if they can be compared with those obtained by other methods. If, however, the estimates of M seem widely divergent from independent estimates, yield predictions from the model should be treated with some scepticism.

b) Fits of the linear relationship:

$$U'_t = \frac{Y_E}{(Z_t - M)} = A - B'(Z_t - M)$$

may be carried out for different trial values of M. This fitting procedure, which can be carried out with predictive or functional linear regression (Ricker 1973), should show departure

from linearity with incorrect trial values for M, with the best fit being obtained when the trial value approximates the true value of M. One simple criterion for goodness of fit is the coefficient of variation of the slope of the linear regression defined by C.V. $= \frac{\text{SE of slope } B'}{B'}$. Other criteria could be used here to determine departure from linearity, and the reader is referred to (e.g.) Draper and Smith (1966). Having chosen the value of M that minimizes the above coefficient of variation, the corresponding values of A and B' will give an estimate of B_∞ and B_∞/r, which will allow estimation of the other parameters.

In connection with this method of fitting, it should be noted that the equilibrium approximation methods of Gulland or Walter (1975) can be applied to the series of Y/F (U') and F values, to correct for departures from equilibrium.

Preliminary Results of the Simulation

Although a major source of bias caused by undetected changes in fishing power of the fleet is avoided by this method, we are as yet less clear about the possible sources of bias in the various estimates of total mortality (Z) given in the literature. Our preliminary simulation results did, however, confirm for the limited cases tested, that Z estimates obtained from catch curve analysis (e.g. Robson and Chapman 1961), and by Pauly (1980) based on mean weight of captured individuals, show good agreement, but that the equation of Beverton and Holt (1956) appears to underestimate Z significantly relative to the others: a result already noted by Pauly (1980), so that simulations with this mortality index underestimated M and F_{MSY}. The other two estimates of Z seemed to provide reasonable estimates of the position of F_{MSY}, in the cases tested, although MSY itself was overestimated when equilibrium was not carried out, especially if the fishing mortality was increased rapidly as F_{MSY} is approached.

Discussion

Although the original impetus for development of these new approaches was a situation where Y_i and $\bar{Z}$ were available, but not f_i, it appears on reflection that this approach offers several distinct advantages, especially but not exclusively for fisheries in developing countries.

In the first place, both of these methods avoid the complete dependence on the collection of total effort data and its subsequent calibration before using in production modeling. This can be very relevant, firstly because of the expense and imprecision of logbook or port interview data, but more important because of the subsequent difficulty of converting nominal effort data into a measure of fishery mortality adjusted for changes in catchability. Brown et al. (1976) showed that in the early years of the industrial fishery in the Northwest Atlantic, fishing efficiency increased substantially on an annual basis due to learning, and by at least 5% per year subsequently. Fishing efficiency tends to increase even in a 'mature' fishery, but despite this, a serious attempt is rarely made to adjust for changes in fishing power before fitting production models (in fact such a correction is only possible if independent estimates of stock size or mortality rate are available, which may favor an estimate of the type described here). The second main problem with existing approaches, using effort and catch rate, concerns the method of fitting the model. Ricker (1975) notes that a regression of the type Y/X against X is statistically suspect: random variability will generate a negative slope even with randomized data (Sissenwine 1978), so that the usual method of fitting production models by plotting catch rate against effort may give spurious estimates of f_{MSY} and MSY, unless the resulting points for Y_T and f_T are observed to fall close to the predicted curve.

Studies of the possible errors and biases that may arise from fitting production models using effort data to fisheries under different conditions of exploitation are contained in Hilborn (1979), based on the application of several formulations of the Graham–Schaefer model to a simulated population with known characteristics. The final conclusions of this study are of importance for all methods of fitting these models, namely:

a) There must be enough contrast in the values assumed by the independent variables "in order to resolve uncertainty about the regression coefficient": (i.e. unless effort levels change over an adequate range of values, the model fit is likely to be spurious).

b) The problems in fitting any production model are most serious when good data collection begins after the stock is already heavily exploited. We note, however, following Brown et al. (1976), that the most serious biases due to unrecorded changes in fishing power of the fleet will also occur in these early years of fishing — one other reason for considering mortality rates directly in the fitting procedure.

c) Hilborn (1979) also notes that there is a need for formal methods to incorporate biological information on the state of the stock obtained by sampling programs into management systems primarily dependent on catch and effort data. We believe the approaches described here will help towards satisfying this last criterion.

Implications for Collection of Fisheries Data

The expense of obtaining catch data by sample survey or census, plus effort data (logbook or port interview) places sufficient strain on the fisheries administration that the addition of analytical data (based on size and age sampling) may be prohibitive. The approach detailed here requires total catch or catch rates by stock, plus an estimate of annual Z (ideally from size samples of the commercial fleet). All of these data series will be needed later in the development of management methods in any case, if we are to make the transition to analytical models which has already occurred in many developed fisheries (e.g. in the North Atlantic and North Pacific). Effort data may still be needed for economical purposes or to regulate and control further development of the fisheries, but with this method the requirement for effort data can be reduced to an up-to-date fishing vessel registry, plus (preferably) an annual series of data on catch rate from a small sample fleet — this will allow us to calculate estimates of q and U. Full coverage of the fleet's fishing effort and its calibration may then no longer be necessary.

Acknowledgments

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BAZIGOS, G. P. 1974. Applied fishery statistics. FAO Fish. Tech. Pap. 135: 104 p.

BEVERTON, R. J. H., AND S. J. HOLT. 1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. Rapp. P. V. Reun. Cons. Perm. Int. Explor. Mer 140: 67–83.

1959. A review of the life spans and mortality rate of fish in nature, and their relation to growth and other physiological characteristics, p. 142–181. *In* G. E. W. Wolstenholme and M. O'Connor [ed.] CIBA Foundation Colloquium on aging. Vol. 5. J. and A. Churchill Ltd., London.

BROWN, B. S., J. A. BRENNAN, H. D. GROSSLEIN, E. G. HEYADAHL, AND R. C. HENNEMUTH. 1976. The effect of fishing on the marine finfish biomass in the Northwest Atlantic from the Gulf of Maine to Cape Hatteras. Int. Comm. Northwest. Atl. Fish. Res. Bull. 12: 49–68.

CLARK, S. H. 1979. Application of bottom trawl survey data to fish stock assessment. (U.S.) Fisheries 4: 9–15.

DERISO, R. B. 1980. Harvesting strategies and parameters estimation for an age-structured model. Can. J. Fish. Aquat. Sci. 37: 268–282.

DRAPER, N. R., AND H. SMITH. 1966. Applied regression analysis. John Wiley & Sons Inc., New York, NY. 407 p.

EVANS, G. T. 1981. The potential collapse of fish stocks in a developing fishery. North Am. J. Fish. Manage. 1: 127–133.

FOX, W. W. 1970. An exponential surplus–yield model for optimizing exploitation of fish populations. Trans. Am. Fish. Soc. 99(1): 80–89.

GRAHAM, M. 1935. Modern theory of exploiting a fishery and application to North Sea trawling. J. Cons. Int. Explor. Mer 10: 264–274.

GULLAND, J. A. 1961. Fishing and the stocks of fish at Iceland. Min. Agric. Fish. Food (U.K.) Fish. Invest. Ser. 11, 23(4): 1–52.

1965. Estimation of mortality rates. Annex to Arctic fishery working group report. (Meeting in Hamburg, January 1965). ICES CM 1965/Doc. No. 3: 9 p. (Mimeo.)

1966. Manual of sampling and statistical methods for fisheries biology. Part 1. Sampling methods. FAO Man. Fish. Sci. No. 3: 87 p.

1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO Man. Fish. Sci. No. 4: 154 p.

HILBORN, R. 1979. Comparison of fisheries control systems that utilize catch and effort data. J. Fish. Res. Board Can. 36: 1477–1489.

JONES, R. 1976. The use of marking data in fish population analysis. FAO Fish. Tech. Pap. 153: 42 p.

1981. The use of length composition data in fish stock assessment (with notes on VPA and cohort analysis). FAO Fish. Circ. 734: 60 p.

LUDVIG, D. 1981. Harvesting strategies for a randomly fluctuating population. J. Cons. Int. Explor. Mer. 39: 168–174.

PALOHEIMO, J. E. 1980. Estimation of mortality rates in fish populations. Trans. Am. Fish. Soc. 109: 378–386.

PAULY, D. 1980. A selection of simple methods for the assessment of tropical fish stocks. FAO Fish. Circ. 729: 54 p.

PELLA, J. J., AND P. K. TOMLINSON. 1969. A generalized stock production model. Bull. Int. Am. Trop. Tuna Comm. 13: 419–496.

POPE, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Res. Bull. ICNAF 9: 65–74.

RICKER, W. E. 1973. Linear regressions in fishing research. J. Fish. Res. Board Can. 30: 409–434.

1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

ROBSON, D. S., AND D. G. CHAPMAN. 1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90(2): 181–189.

ROTHSCHILD, B. J., AND D. S. ROBSON. 1972. The use of concentration indices in fisheries. Fish. Bull. NOAA/NMFS 70: 511–514.

SCHAEFER, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial fisheries. Bull. Int. Am. Trop. Tuna Comm. 1(2): 26–56.

SCHNUTE, J. 1977. Improved estimates from the Schaefer production model. Theoretical considerations. J. Fish. Res. Board Can. 34: 583–603.

SHEPHERD, J. G. 1982. A family of general production curves for exploited populations. Math. Biosci. (In press)

SISSENWINE, M. P. 1978. Is MSY an adequate foundation for optimal yield? (U.S.) Fisheries 3: 22–42.

SSENTONGO, G. W., AND P. LARKIN. 1973. Some simple methods of estimating mortality rates of exploited fish populations. J. Fish. Res. Board Can. 30: 695–698.

UHLER, R. S. 1979. Least squares regression estimates of the Schaefer production model: some Monte Carlo simulation results. Can. J. Fish. Aquat. Sci. 37: 1284–1294.

VAN SICKLE, J. 1977. Mortality rates from size distributions. The application of a conservation law. Oecologia (Berlin) 27: 311–318.

WALTER, G. G. 1975. Graphical models for estimating parameters in simple models of fisheries. J. Fish. Res. Board. Can. 32: 2163–2168.

Le Panache du Saguenay

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LEBEL, J., E. PELLETIER, M. BERGERON, N. BELZILE ET G. MARQUIS. 1983. Le panache du Saguenay. Can. J. Fish. Aquat. Sci. 40: 52 – 60.

La forte différence d'alcalinité totale existant entre les eaux douces du fleuve Saint-Laurent (1,475 mmol·kg^{-1}) et celles de la rivière Saguenay (0,134 mmol·kg^{-1}) nous ont permis de localiser dans l'estuaire du Saint-Laurent la région sous l'influence du Saguenay. Cette méthode présente l'avantage par rapport aux mesures classiques de salinité et de température de donner des résultats indépendants de la remontée d'eau profonde dans cette région. Les données furent recueillies lors d'une mission océanographique au cours de laquelle 33 stations ont été occupées à l'étale de marée basse et 23 à l'étale de marée haute. Les résultats obtenus montrent qu'à marée basse les eaux du Saguenay forment au centre du chenal un panache de plus de 10 km que l'on peut déceler même à 25 m tandis qu'à marée haute ce panache est restreint à la couche de surface alors que les eaux du Saguenay sont refoulées par-dessus le seuil.

Mots clés: alcalinité, estuaire, mélange, Saguenay, Saint-Laurent

LEBEL, J., E. PELLETIER, M. BERGERON, N. BELZILE ET G. MARQUIS. 1983. Le panache du Saguenay. Can. J. Fish. Aquat. Sci. 40: 52 – 60.

The large difference between the alkalinity of the fresh waters of the St. Lawrence River (1.475 mmol·kg^{-1}) and the Saguenay River (0.134 mmol·kg^{-1}) was used to locate the region on the St. Lawrence estuary which is under the influence of the Saguenay River. This method has the advantage over classical measurements such as salinity and temperature that it is independent of the upwelling of deep water in this region. Data was obtained in the St. Lawrence estuary near the mouth of the Saguenay fjord using a network of 33 stations at slack low tide and 23 stations at slack high tide. The results show that, at low tide, Saguenay water forms a plume which extends more than 10 km from the mouth of the fjord into the estuary. At high tide the plume is restricted to the surface layer as the Saguenay waters are pushed back into the fjord.

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LA rivière Saguenay traverse une ancienne vallée glaciaire surcreusée (jusqu'à 275 m) sur une distance de plus de 100 km avant de se déverser (débit annuel moyen: 1,3 × 10^3 m^3·s^{-1} (D'Anglejan 1970)) dans l'estuaire du Saint-Laurent au-dessus d'un seuil où la profondeur n'est que de 20 m (fig. 1) (Drainville 1968).

L'influence de la marée combinée à la topographie accidentée du fond près de son embouchure confère à cette région un régime de circulation particulier. D'une part, le massif de l'Ilet Rouge qui divise le Saint-Laurent en deux canaux et la remontée brusque du chenal Laurentien vers le seuil perturbent la circulation estuarienne de l'endroit. Ce seuil provoque une remontée en surface des eaux intermédiaires, froides et salées, originaires du golfe Saint-Laurent et de l'Atlantique nord (Lauzier et Trites 1958; Ingram 1979). D'autre part, l'importance des marées introduit de forts courants qui au jusant peuvent atteindre 3 m·s^{-1}.

Des travaux récents (Seibert et al. 1979) ont montré la régénération des eaux profondes du fjord du Saguenay à partir des eaux provenant de la couche intermédiaire du chenal Laurentien. Ce renouvellement explique entre autres la bonne oxygénation des eaux du fond (≃6 mL·L^{-1}).

C'est pourquoi le mélange des eaux originaires du fleuve Saint-Laurent avec celles de la rivière Saguenay conjugué à la forte turbulence dans la région extérieure au seuil rendent difficile l'identification de la zone d'écoulement du Saguenay (le panache) par les mesures classiques de salinité et de température.

Par contre, la forte différence d'alcalinité totale existant entre les eaux douces du fleuve Saint-Laurent (≃1,4 mmol·kg^{-1}) et celles de la rivière Saguenay (≃0,1 mmol·kg^{-1}) permet d'utiliser l'alcalinité totale comme indicateur de mélange (Pelletier et Lebel 1980).

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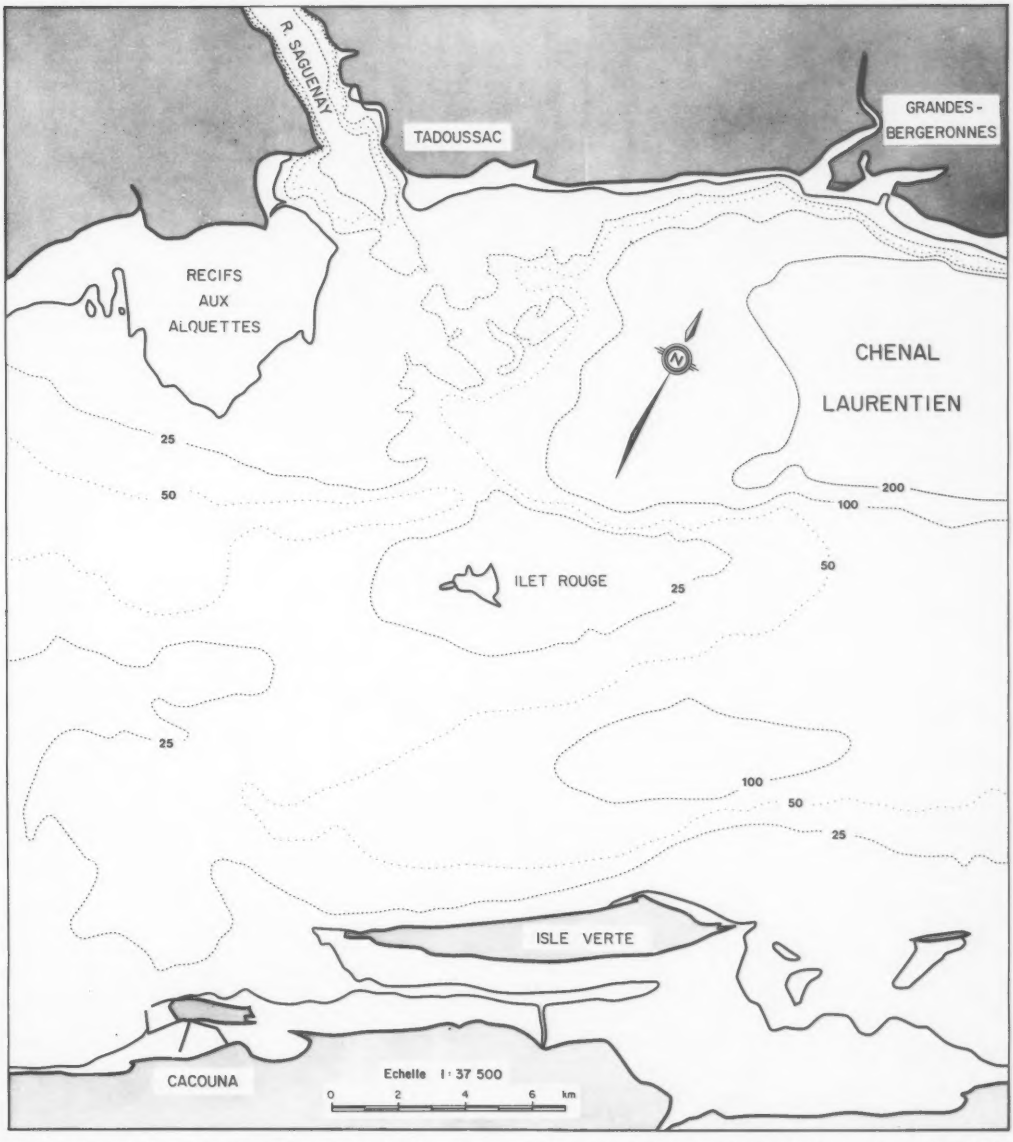


FIG. 1. Partie de l'estuaire du Saint-Laurent à l'embouchure du Saguenay. Les régions sombres représentent les berges alors que les régions grises indiquent les espaces découverts à marée basse.

Matériel et méthodes

Au cours d'une mission en novembre 1979, nous avons occupé 33 stations à l'étale de jusant et 23 stations à l'étale de flot. Sur les échantillons recueillis, nous avons mesuré la salinité et l'alcalinité totale, lesquelles données combinées à la mesure de la température ont été utilisées pour déterminer le panache correspondant à l'écoulement du Saguenay dans l'estuaire du Saint-Laurent.

La campagne d'échantillonnage a eu lieu pendant la période de vives eaux du 5 au 10 novembre inclusivement. Nous avons prélevé les échantillons à l'aide de bouteilles Niskin de

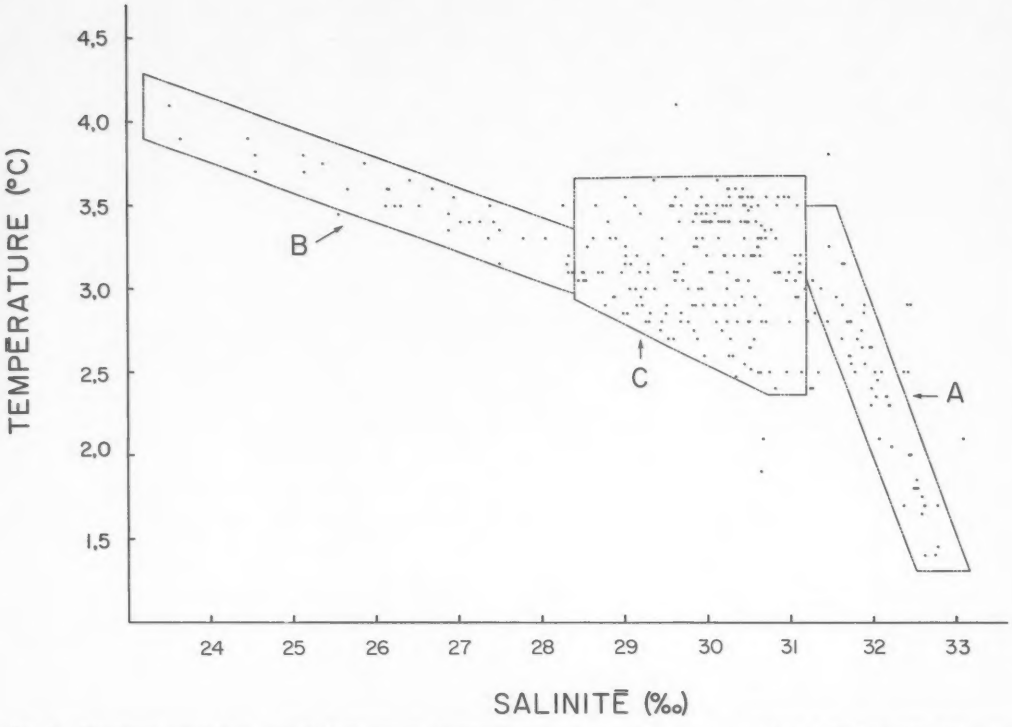


FIG. 2. Diagramme température–salinité. Nous pouvons identifier deux masses d'eau distinctes: la masse d'eau *A*, froide et salée et la masse d'eau *B* plus douce et moins froide formant toutes deux le mélange *C*.

5 L munies de thermomètres à renversement, durant les périodes de 2 h correspondant à peu près à l'étale de marée haute ou à l'étale de marée basse. Nous avions planifié les déplacements du bateau de façon à couvrir plusieurs stations lors d'une même marée, nous déplaçant d'une région à une autre pendant les périodes de flux et de reflux.

Nous avons mesuré la salinité à l'aide d'un salinomètre Guildline offrant une précision de l'ordre de ±0,003 ‰ et l'alcalinité totale par titrage potentiométrique (Edmond 1970) d'échantillons filtrés et thermostatés à 25°C. Nous avons obtenu pour l'ensemble des dosages une déviation maximale de ±0,006 mmol·kg^{-1}.

Résultats et discussion

Nous avons regroupé toutes les mesures de température et de salinité sur un seul diagramme (fig. 2). Sur celui-ci, nous pouvons identifier deux masses d'eau distinctes: la masse d'eau froide *A* (de 1 à 3,5°C) et salée (de 31,5 à 33 ‰) correspondant à la couche d'eau intermédiaire de l'estuaire maritime et du golfe (Lauzier et Trites 1958; Ingram 1979) qui remonte à la fin du chenal Laurentien et se mélange avec une masse d'eau *B* moins froide (de 2,5 à 4°C) et moins salée (de 23 à 30 ‰). La masse d'eau la moins salée (*B*) est constituée par l'apport d'eau douce du Saguenay et du Saint-Laurent mais les seules données de température et de salinité ne permettent pas d'identifier l'origine de l'eau douce donnant lieu à la masse *B*. Nous notons aussi un troisième groupe de données (*C*) qui représente le mélange des eaux marines (*A*) aux eaux estuariennes (*B*). Ainsi donc, si nous traçions les isohalines et les isothermes pour chacune des profondeurs, les courbes obtenues seraient représentatives de la dilution des eaux marines par des eaux estuariennes qui proviennent à la fois du Saint-Laurent et du Saguenay. Ces résultats permettraient d'observer la zone de remontée dans cette région mais on ne pourrait pas attribuer de façon certaine à l'arrivée d'eau du Saguenay le panache tracé par les isohalines.

Par contre, le diagramme alcalinité totale-salinité (fig. 3) est beaucoup plus éloquent. D'abord, dans un milieu estuarien, l'alcalinité totale est un paramètre beaucoup mieux conservé que la température de sorte que les points sont plus groupés le long de quelques droites. Comme sur le diagramme *T*–*S*, on observe à nouveau la masse d'eau marine (*A*) de même que des eaux mélangées (*C*). Mais, dans la masse d'eau estuarienne *B*, on peut distinguer les eaux du Saint-Laurent à alcalinité élevée (B_1) et les eaux originaires du Saguenay à faible alcalinité (B_2). Nous avons donc le cas précis où pour un mélange de trois masses d'eau (marine, eau

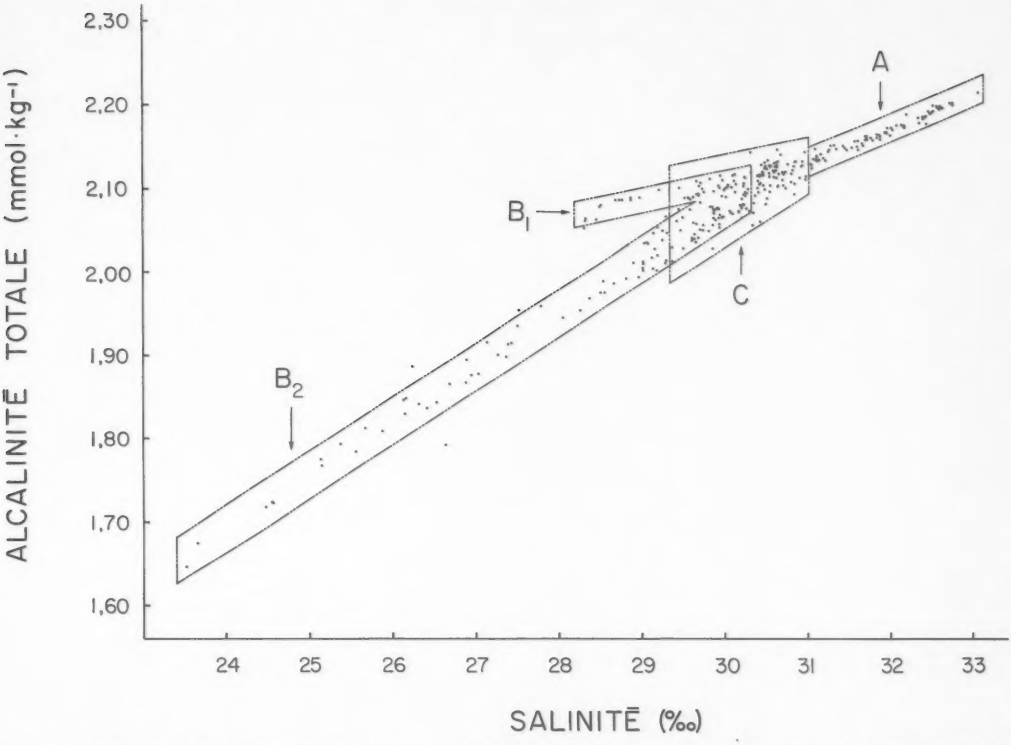


FIG. 3. Diagramme alcalinité totale–salinité. Nous pouvons identifier trois masses d'eau: l'eau d'origine marine *A*, l'eau provenant de la dilution de l'eau douce du Saint-Laurent B_1, et l'eau provenant de la dilution de l'eau douce du Saguenay B_2.

douce du Saint-Laurent et eau douce de la rivière Saguenay), l'on dispose de deux grandeurs conservatrices, l'alcalinité totale (AT) et la salinité (S), de sorte que l'on peut facilement calculer la contribution de chacune des masses d'eau en résolvant le système suivant en chaque point:

$$(1)\quad AT = (X_1 \cdot AT_1) + (X_2 \cdot AT_2) + (X_3 \cdot AT_3)$$

$$(2)\quad S = (X_1 \cdot S_1) + (X_2 \cdot S_2) + (X_3 \cdot S_3)$$

$$(3)\quad X_1 + X_2 + X_3 = 1$$

pour lequel (AT_1, S_1), (AT_2, S_2) et (AT_3, S_3) représentent les caractéristiques de chacune des masses d'eau et X_1, X_2 et X_3 les fractions volumiques formant un mélange donné. Le tableau 1 donne la valeur de chacun des paramètres des équations (1) et (2) pour la région étudiée. Nous fixons à 32,5 ‰ la salinité des eaux marines participant au mélange puisque, dans l'estuaire du Saint-Laurent, cette valeur représente la limite du mélange entre les eaux fluviales et les eaux marines (Pelletier et Lebel 1979) au delà de laquelle la contribution ionique des eaux du fleuve devient négligeable (Poisson et al. 1980).

Nous avons utilisé les valeurs du tableau 1 pour calculer en chaque point de prélèvement la fraction volumique (en %) des eaux douces de la rivière Saguenay. La figure 4 montre pour chaque profondeur, à l'étale de jusant, les lignes d'isocomposition qui tracent le panache du Saguenay dans l'estuaire du Saint-Laurent. Nous remarquons que, à marée basse, les eaux du Saguenay forment une langue qui avance vers l'est, suivant le courant, sur plus de 10 km dans le Saint-Laurent à égale distance de la côte nord et de l'Ilet Rouge. Cet écoulement plus important en surface, diminue avec la profondeur mais est toujours présent même à une profondeur sous le niveau du seuil, à 25 m, où l'eau douce du

TABLEAU 1. Alcalinités et salinités caractéristiques des eaux se mélangeant dans la région étudiée.

Eau	Salinité, ‰	Alcalinité totale (AT), mmol·kg^{-1}
Eau douce du Saguenay	≃0	0,134[a]
Eau douce du Saint-Laurent	≃0	1,418[a]
Eau marine correspondant à la couche intermédiaire de l'Estuaire maritime du Saint-Laurent	32,5	2,105[b]

[a]Valeurs mesurées.
[b]Pelletier et Lebel 1979.

a) % eau douce du Saguenay
b) Salinité (‰)
c) Température (°C)
Surface
2 m
5 m
Tadoussac

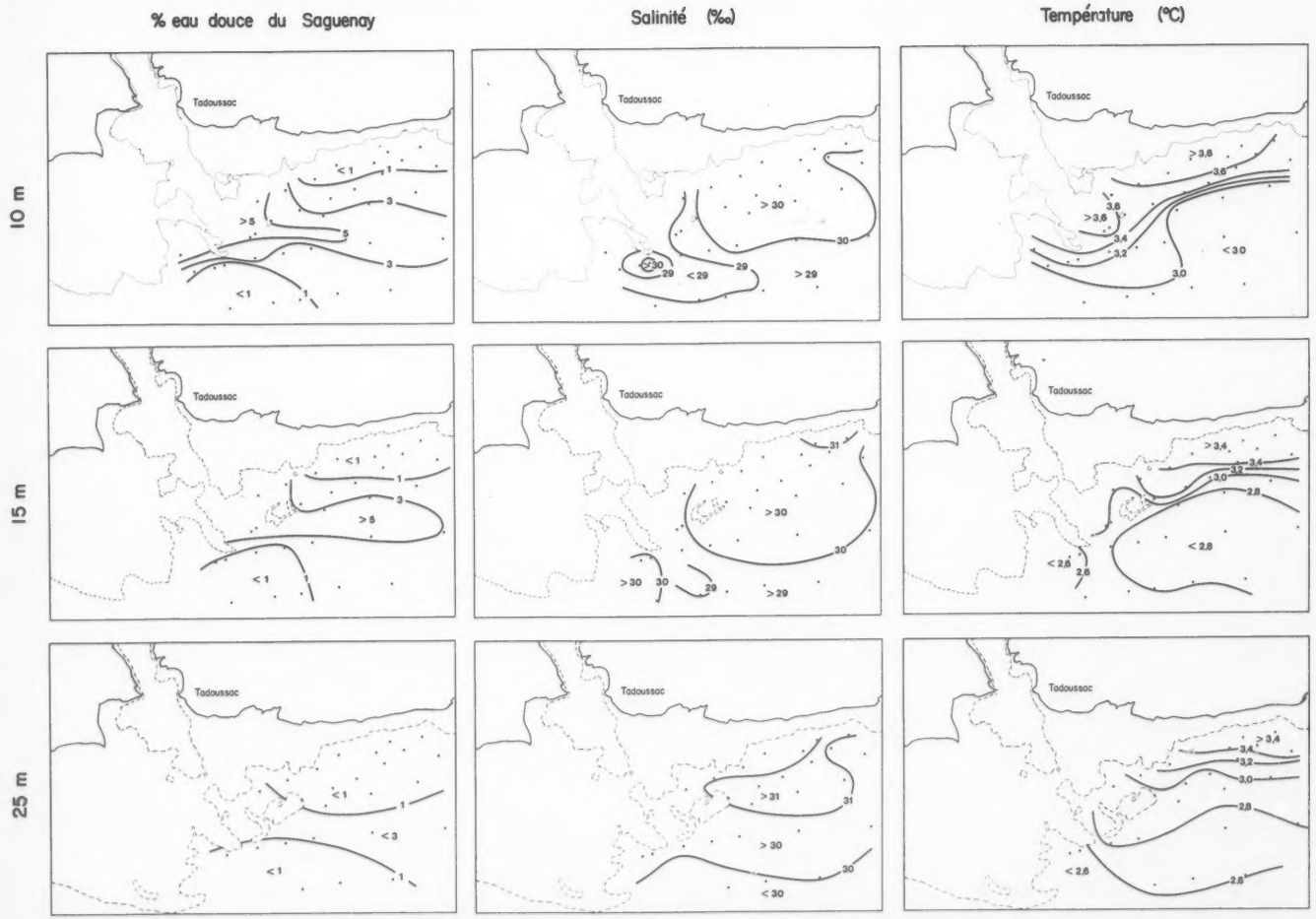
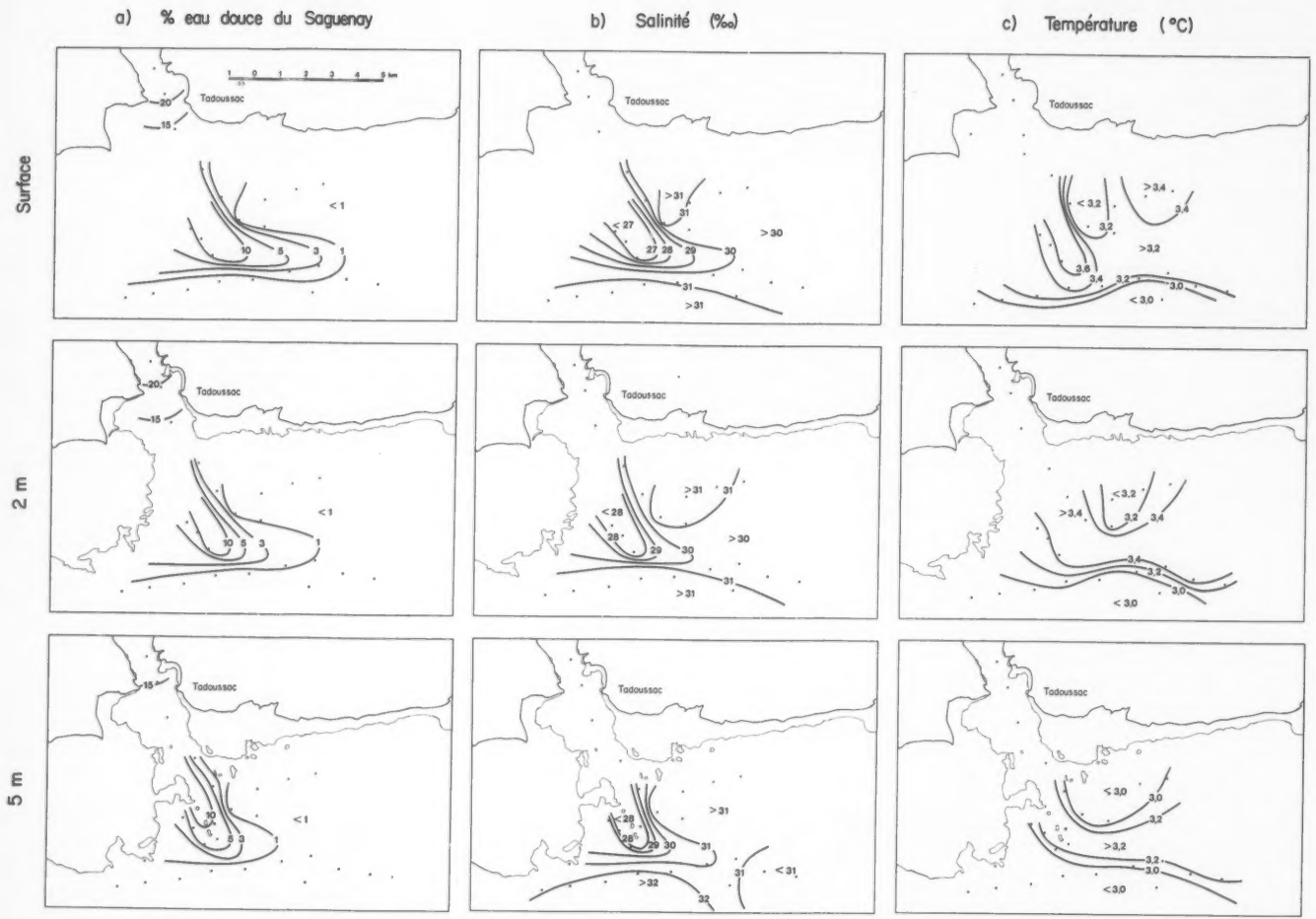


FIG. 4. Résultats obtenus à l'étale de jusant pour chacune des profondeurs. (a) Lignes d'iso-composition donnant le pourcentage d'eau douce du Saguenay; (b) Lignes isohalines; (c) Lignes isothermes.


a) % eau douce du Saguenay
b) Salinité (‰)
c) Température (°C)
Surface
2 m
5 m
Tadoussac
1 0 1 2 3 4 5 km
0.5
20
15
10
5
3
1
< 1
> 31
31
< 27
27
28
29
30
> 30
> 32
32
< 31
> 3,4
3,4
< 3,2
3,2
> 3,2
3,6
3,4
3,2
3,0
< 3,0

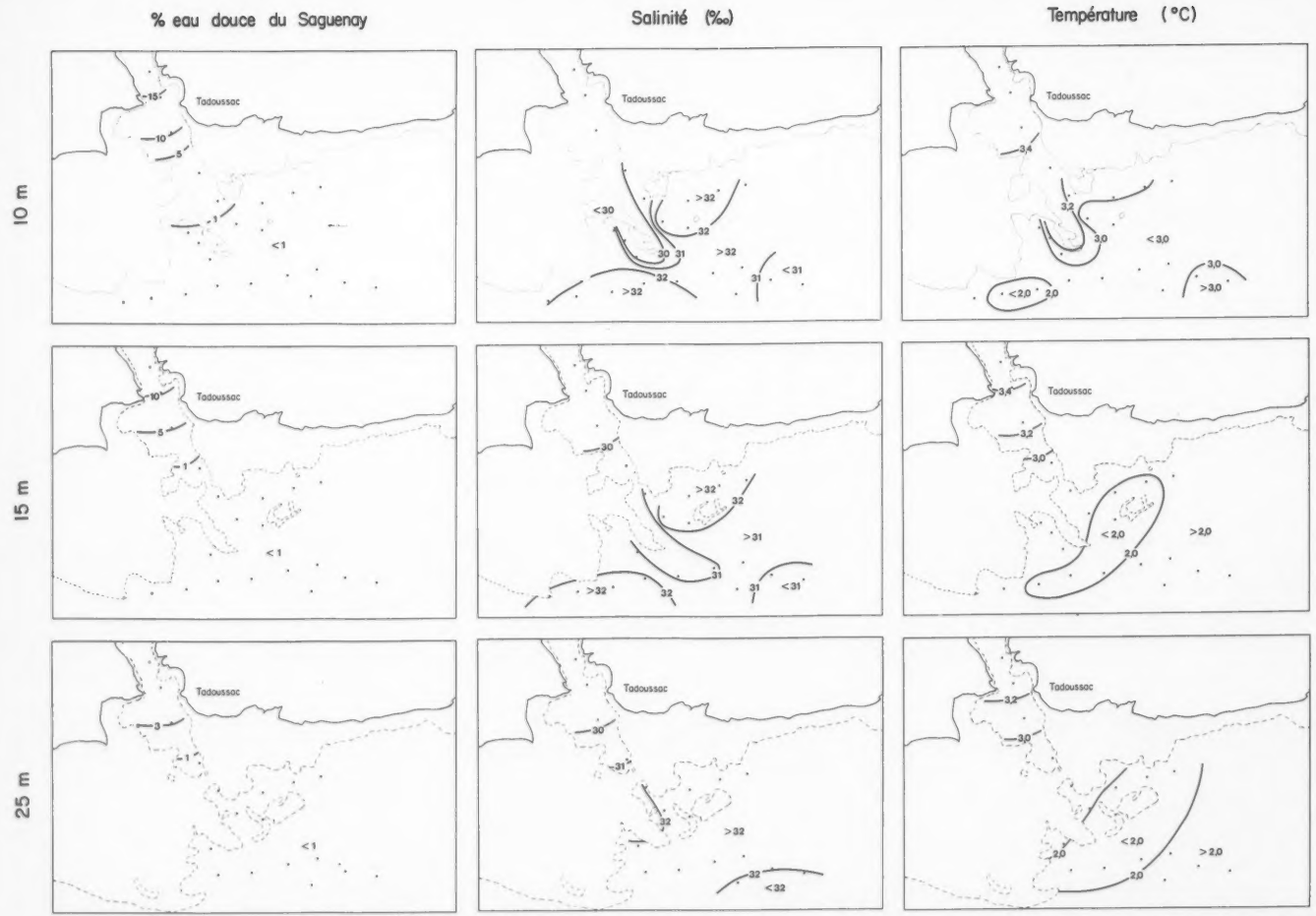


FIG. 5. Résultats obtenus à l'étale de flot pour chacune des profondeurs. (a) Lignes d'iso-composition donnant le pourcentage d'eau douce du Saguenay; (b) Lignes isohalines; (c) Lignes isothermes.

Saguenay représente encore de 1 à 3 % du mélange. On observe une présence plus importante des eaux du Saguenay au centre du chenal; la région près de la côte et de l'Ilet Rouge subit la remontée des eaux marines comme nous le révèle non seulement l'absence d'eau douce du Saguenay (% < 1) mais aussi la présence d'eau plus froide et plus salée. Par contre, la complexité des données $T-S$ ne permet pas aux isothermes ni aux isohalines d'être vraiment représentatives des masses d'eaux participantes de sorte que les graphiques 4b et 4c n'ont pas de signification claire comme le sont les données du graphique 4a.

Les données de composition recueillies à l'étale de flot, portées sur la figure 5a, décrivent un panache plus petit qu'à marée basse et restreint aux eaux de surface alors que pour les profondeurs supérieures à 10 m les eaux du Saguenay sont retenues à l'intérieur du fjord. Ces résultats sont très différents de ce que peuvent laisser croire les isohalines et les isothermes. En effet, les isohalines (fig. 5b) délimitent assez bien le panache en surface alors qu'au fond elles indiquent la présence sur le côté estuarien du seuil d'une enclave d'eau plus douce qui provient du fleuve Saint-Laurent lui-même. L'image présentée par les isothermes (fig. 5c) est encore plus perturbée. D'abord en surface, c'est la remontée des eaux profondes et froides qui domine toute la représentation puisque des masses d'eaux froides (< 3,2°C) viennent s'immiscer de chaque côté de l'écoulement des eaux douces. Déjà à 2 m sous la surface, seule semble dominer cette remontée, les isothermes se retrouvant parallèles à la côte alors que plus au fond, ces données n'indiquent plus que la présence devant le seuil d'une masse d'eau pour laquelle la température est inférieure à 2,0°C.

En fait, nous avons deux séries de résultats, dérivés pour les uns de la mesure de l'alcalinité et, pour les autres, de la mesure de la température qui apportent des conclusions de signification et de valeur différentes: alors que les mesures d'alcalinité et les calculs de la fraction volumique de l'eau douce du Saguenay permettent une parfaite identification du panache de celui-ci dans l'estuaire du Saint-Laurent, les isothermes de cette région sont d'une interprétation plus malaisée. Elles sont à relier à la remontée des eaux marines froides, phénomène qui se trouve être beaucoup plus important à l'étale de flot qu'à l'étale de jusant.

Ainsi, les données d'alcalinité totale permettent une meilleure description de l'écoulement du Saguenay dans l'estuaire du Saint-Laurent. Cette description complète les données hydrologiques disponibles et devrait permettre aux océanographes physiciens d'améliorer leur modèle de circulation dans cette région. Un tel modèle permettra entre autres de prévoir le devenir d'importantes quantités de produits toxiques et solubles pouvant accidentellement être déversées dans le fjord du Saguenay et de prendre plus adéquatement les mesures de protection pour les régions menacées.

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D'Anglejan, B. F. 1970. Studies on particulate suspended matter in the Gulf of St. Lawrence. Manuscript Report, Vol. 17, Marine Science Centre, McGill University, Montréal. 51 p.

Drainville, G. 1968. Le Fjord du Saguenay: contribution à l'océanographie. Naturaliste Can. 95: 809–855.

Edmond, J. M. 1970. High precision determination of titration alkalinity and total carbon dioxide content of sea water by potentiometric titration. Deep-Sea Res. 17: 737–750.

Ingram, R. G. 1979. Water mass modification in the St. Lawrence Estuary. Naturaliste Can. 106: 45–54.

Lauzier, L. M., et R. W. Trites. 1958. The deep waters in the Laurentian Channel. J. Fish. Res. Board Can. 15: 1247–1257.

Pelletier, E., et J. Lebel. 1979. Hydrochemistry of dissolved inorganic carbon in the St. Lawrence Estuary (Canada). Estuarine Coastal Mar. Sci. 9: 785–795.

1980. L'alcalinité totale comme indicateur de mélange dans un milieu estuarien. Can. J. Earth. Sci. 17: 978–984.

Poisson, A., J. Lebel et C. Brunet. 1980. Influence of local variations in the ionic ratios on the density of seawater in the St. Lawrence area. Deep-Sea Res. 27: 763–781.

Seibert, G. H., R. W. Trites et S. J. Reid. 1979. Deepwater exchange processes in the Saguenay Fjord. J. Fish. Res. Board Can. 36: 42–53.

Manipulation of the Seasonal Reproductive Cycle of the Landlocked Atlantic Salmon (*Salmo salar*) by LHRH Analogues Administered at Various Stages of Gonadal Development[1]

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Pellets designed for continuous, long-term, oligopeptide, hormone delivery were implanted into the adult landlocked Atlantic salmon (*Salmo salar*) to investigate the effects of LHRH agonist analogue (LHRH-A) upon the reproductive system. Chronic elevations in plasma gonadotropin were observed in experimental fish at a variety of stages of reproductive development. Synthesis of pituitary gonadotropin was also evoked in sexually regressed fish and fish undergoing gonadal recrudescence, but the already elevated level of pituitary GtH observed in prespawning and spawning salmon was not augmented. In prespawning fish, the events of ovulation and spermiation were accelerated by LHRH-A treatment. The LHRH-A hormone treatment also increased milt volume and the duration of spermiation in ripe males. In sexually regressed males LHRH-A treatment did not induce the advanced phases of spermatogenesis but some testicular stimulation was indicated by the presence of increased numbers of B-type spermatogonia and enlargement of the lumen of lobules. The gonadal response to LHRH-A treatment during the rapid phase of gonad recrudescence differed in males and females. Based upon the changes in GSI, the LHRH analogue accelerated vitellogenic development of the ovaries in females; in males, however, the GSI was significantly reduced following LHRH-A administration. Whereas, it seems clear that a long acting preparation containing LHRH-A can be successfully used in prespawning fishes to advance the final events of gonadal maturation and initiate spawning, further studies are necessary to evaluate the potential of LHRH agonists to either stimulate or inhibit the reproductive development of fish at other stages of the seasonal reproductive cycle.

Key words: fish, teleosts, landlocked salmon, LHRH analogues, gonadotropic hormone releasing hormones, seasonal reproductive cycle, gonad development, spawning

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Des capsules conçues pour la diffusion continue à long terme de l'hormone oligopeptidique ont été implantées dans des saumons atlantiques (*Salmo salar*) adultes de l'intérieur, dans le but d'étudier l'incidence de l'analogue agoniste de l'hormone de déclenchement de l'hormone lutéinotrophe (LHRH-A) sur le système reproducteur. Le LHRH-A a causé des augmentations chroniques de la gonadotropine plasmatique chez les poissons expérimentaux à divers stades du développement reproductif. La synthèse de gonadotropine pituitaire a aussi été provoquée chez les poissons sexuellement régressés et les poissons en stade de

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recrudescence gonadique, mais le niveau déjà élevé d'hormone gonadotrope (GtH) pituitaire noté chez les saumons avant et pendant la fraie n'a pas augmenté. Dans le premier cas, le LHRH-A a accéléré l'ovulation et la spermiation et a entraîné une augmentation du volume de laitance et de la durée de la spermiation chez les mâles pleins. Chez les mâles sexuellement régressés, le LHRH-A n'a pas provoqué les phases avancées de la spermatogénèse, mais une certaine stimulation testiculaire a été révélée par la présence d'un nombre accru de spermatogonies de type B et la dilatation du lumen des lobules. Au cours de la phase rapide de recrudescence gonadique, l'analogue LHRH-A a accéléré le développement vitellogène des ovaires des femelles et a réduit de façon significative l'IGS chez les mâles. Il semble qu'une préparation de LHRH-A à effet prolongé accélère avec succès les dernières étapes de la maturation des gonades et déclenche la fraie chez les poissons prénuptiaux, mais il faudra des études plus poussées pour évaluer le potentiel stimulateur ou inhibiteur des agonistes LHRH sur le développement reproductif des poissons pendant les autres stades de cette phase.

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EFFICIENT fish culture operations are necessarily based upon predictable seed fish supplies which require successful management of the brood stock reproductive cycles. However, under captive conditions, the natural reproductive cycles of adult fish may become irregular or disrupted. Solutions to some of these problems with reproduction at fish farms have been found in applications of endocrinology (Lam 1982).

Because luteinizing hormone releasing hormone (LHRH) is an oligopeptide which can be produced in large quantities at relatively low cost, this substance has been receiving increased attention as a potential agent for controlling reproductive events in brood stock fishes. Regulating reproductive cycles with LHRH would obviate the need for treating fish with expensive pituitary preparations which may produce unpredictable results or have harmful side effects by possibly inducing antibody formation. To date, successful manipulation of fish reproduction with LHRH has been limited, most likely because of rapid clearance or inactivation of such a small oligopeptide hormone. Multiple injections of LHRH might be useful, but in addition to increasing the costs of labor and materials, such handling procedures may not be practical, especially with fish sensitive to stress. There is a need for long-acting/slow release formulations of LHRH which would maximize the biological effectiveness of the peptide hormone administration.

Recently, a compacted cholesterol pellet matrix was formulated by Kent et al. (1980) and used in mammals to provide sustained release of water-soluble peptidic substances such as LHRH or LHRH agonist analogues (LHRH-A) for periods exceeding 30 d. The present experiments were conducted to study the influence of this kind of pellet containing (LHRH-A) upon reproductive cycles in the landlocked Atlantic salmon (*Salmo salar*). In addition to attempts to induce spawning, we also investigated the ability of LHRH analogues administered in this manner to initiate reproductive development in fish with regressed gonads and to stimulate the reproductive system during the rapid phase of gonadal recrudescence.

Materials and Methods

A laboratory stock of adult landlocked salmon were maintained in ambient freshwater and exposed to simulated natural photoperiods appropriate for the time of year. The fish were spawned by hand in the fall and were fed a moist pellet diet (pellet composition in percent: moisture 48, protein 34, lipid 6, carbohydrate 7, ash 5) throughout the year. We selected male and female salmon of 72 and 171 g average body weight, respectively, which had completed at least one previous reproductive cycle in the laboratory. Five individual experiments lasting 3 or 4 wk were conducted using the cholesterol pellets containing one of two LHRH analogues. The seasonal effect of LHRH-A treatment was investigated by testing the responsiveness of salmon at four different stages of gonadal development:

Experiment 1 — Regressed male salmon (March – April)
Experiment 2 — Recrudescing male and female salmon (August – September)
Experiment 3 — Prespawning male and female salmon (September – October)
Experiment 4 — Prespawning female salmon (October – November)
Experiment 5 — Spawning male salmon (January – February).

At the beginning of each experiment the fish scheduled for LHRH-A treatment received a single pellet, about 3 × 3 mm, implanted surgically into the perivisceral cavity. Sham control fish also underwent the surgical procedures without receiving the pellet implant. Because the supply of hormone pellets was limited, two different 'superactive' LHRH analogues were tested during the series of five experiments. In experiments 1 and 5, pellets containing 125 μg [6-(D-2-naphthylalanine)] LHRH (D-Nal(2)^6-LHRH) were used; pellets containing 125 μg [6-(D-Trp-desGly-10-ethylamide)]-LHRH (D-Trp^{6}EA-LHRH) were implanted into the experimental fish in experiments 2, 3, and 4. The relative biological activities of these peptides have been tested in vivo in rats; D-Trp^{6}EA-LHRH and D-Nal(2)^6-LHRH are ~100 and 200 times more potent than LHRH itself (Nestor et al. 1982).

The plasma and pituitary gonadotropic hormone (GtH) levels were determined by radioimmunoassay methods previously described (Crim et al. 1975). Direct gonad analysis was conducted on microscopic sections obtained from tissues fixed in Bouin's fluid and prepared according to standard paraffin histological procedures. The gonadosomatic index (GSI) was derived by dividing the weight of the testes by body

TABLE 1. Influence of D-Nal(2)^6-LHRH treatment on gonadosomatic index (GSI) and plasma and pituitary gonadotropin in the sexually regressed male landlocked salmon (March–April).[a]

Treatment	N	GSI (%)	Plasma GtH, ng/mL		Pituitary GtH, ng
			2 wk	4 wk	
Initial control	3	0.25±0.03	(0.69±0.04)		—
Sham control	5	0.26±0.05	0.66±0.04	0.64±0.08	396.5±116.9
LHRH-A pellet	5	0.45±0.06	3.16±0.51	4.10±1.05	2265.4±347.6

[a]Values are $\bar{x}$ ± SEM.

weight and multiplying the results by 100. For statistical analysis one-way ANOVA was used followed by Student–Neuman–Keuls testing of mean ranges.

Results

EXPERIMENT 1 — REGRESSED MALE SALMON (TABLE 1)

In March the testes of postspawned males are regressed and the GSI is low. The GSI of sexually regressed males was not significantly increased after 4 wk of D-Nal(2)^6-LHRH treatment; however, the tendency in this group towards an augmentation of GSI was noted. Microscopic analysis of the testes revealed that large numbers of A-type spermatogonia lined compact seminiferous lobules of control males. Mitotic figures were observed in a few spermatogonial cells. The testes of one control male contained isolated pockets of spermatozoa presumably remaining from the previous spawning period. In another control male lobules contained about equal numbers of A- and B-type spermatogonia. Although D-Nal(2)^6-LHRH treatment did not induce advanced stages of spermatogenesis, some changes in the testicular lobules were observed in the experimental males. Thus, B-type spermatogonia appeared in greater numbers in four fish, and many of the lobules were expanded at the center. In one D-Nal(2)^6-LHRH-treated male, large numbers of spermatozoa filled expanded lobules, but the intermediate cell types (e.g. spermatocytes and spermatids) were not present.

In sexually regressed males pituitary GtH is relatively low (nanograms) in April. Compared with pituitary GtH in sham controls, a marked increase in pituitary GtH occurred after 4 wk of a single application of D-Nal(2)^6-LHRH ($P < 0.01$). Whereas plasma GtH remained low with little variation in control males, experimental males showed elevated plasma GtH at 2 and 4 wk after D-Nal(2)^6-LHRH treatment. It appeared from this study that chronic GtH release is produced by this method of LHRH-A administration.

EXPERIMENT 2 — RECRUDESCING MALE AND FEMALE SALMON (TABLE 2)

The landlocked salmon enters into a phase of rapid gonadal development beginning in August. In both groups of males and females the GSI significantly increased ($P < 0.05$) during the 3-wk-experimental period (GSI of sham controls compared with initial controls). At the end of the experiment in September spermatogenesis was clearly underway in all sham control males. Spermatocytes and spermatids were the dominant cell types but spermatozoa were present in the lumen of a few lobules. The GSI of males treated with D-Trp^{6}EA-LHRH was significantly reduced ($P < 0.01$). Microscopically, the lobules of these males contained large numbers of spermatids and spermatozoa with a concomitant decrease in the proportion of spermatocytes. In females D-Trp^{6}EA-LHRH treatment significantly increased the GSI ($P < 0.05$) suggesting that vitellogenic development was accelerated. After 3 wk of LHRH-A treatment at this phase of the reproductive cycle, neither spermiation nor ovulation was observed.

The influence of LHRH-A administration on pituitary and plasma GtH levels was similar in males and females. Pituitary GtH was elevated ($P < 0.01$) by D-Trp^{6}EA-LHRH treatment. Plasma GtH in sham controls remained low throughout this experiment even though gonadal recrudescence was evident. After D-Trp^{6}EA-LHRH treatment plasma GtH increased and remained elevated for the duration of the experimental period. In females higher plasma GtH levels were achieved at 3 wk compared with 1 wk after the initiation of D-Trp^{6}EA-LHRH treatment.

EXPERIMENT 3 — PRESPAWNING MALE AND FEMALE SALMON (TABLE 3)

The GSI is relatively advanced in September in males and also in females which showed further vitellogenic development during the experimental period (GSI sham controls > initial controls, $P < 0.01$). A microscopic examination of testes sections showed that testicular lobules obtained from initial control males were populated primarily with spermatocytes and spermatids at the beginning of the study. A few lobules also contained spermatozoa. In October testes lobules of sham control males contained about equal numbers of spermatocytes, spermatids, and spermatozoa. Spermiation was detectable in just one sham control male when the experiment was terminated. Sexual development of prespawning males was advanced by D-Trp^{6}EA-LHRH treatment as all males receiving the pelleted hormone were spermiating in October. Stimulation of spermatogenesis was further indicated by the effect of D-Trp^{6}EA-LHRH on testes histology which showed that testes lobules in experimental males contained greater numbers of spermatids and spermatozoa and fewer spermatocytes compared with sham control males. Previous records indicated that spawning of this stock of landlocked salmon normally takes place in late November or December. Therefore, according to expectations, no ovulations were recorded in sham control females in October.

TABLE 2. Influence of D-Trp^{6}EA-LHRH treatment on GSI and plasma and pituitary GtH in the landlocked salmon during the gonad recrudescent phase (August–September).[a]

Treatment	N	GSI (%)	Plasma GtH, ng/mL 1 wk	Plasma GtH, ng/mL 3 wk	Pituitary GtH, ng
			Males		
Initial control	5	1.1±0.1	—	—	—
Sham control	5	3.2±0.3	1.09±0.02	1.00±0.04	438±152
LHRH-A pellet	5	1.4±0.2	9.51±1.23	10.54±1.44	5220±750
			Females		
Initial control	5	8.2±0.5	—	—	—
Sham control	5	12.3±1.3	1.28±0.03	0.99±0.03	631±52
LHRH-A pellet	5	15.6±1.1	3.21±0.72	18.70±4.28	8730±1130

[a]Values are $\bar{x}$ ± SEM.

TABLE 3. Influence of D-Trp^{6}EA-LHRH treatment on GSI and plasma and pituitary GtH in the prespawning landlocked salmon (September–October).[a]

Treatment	N	GSI (%)	Plasma GtH, ng/mL 1 wk	Plasma GtH, ng/mL 3 wk	Pituitary GtH, µg
			Males		
Initial control	3	5.6±0.22	(1.01±0.08)		0.39±0.05
Sham control	5	6.94±0.76	0.96±0.06	0.92±0.05	3.31±0.93
LHRH-A pellet	4	5.91±0.35	23.8±1.40	39.2±6.5	8.46±2.08
			Females		
Initial control	3	13.3±0.45	(0.87±0.11)		0.83±0.27
Sham control	5	16.2±0.60	0.92±0.05	0.94±0.04	2.89±0.65
LHRH-A pellet	6	[b]	10.6±1.59	23.0±4.7	10.09±1.05

[a]Values are $\bar{x}$ ± SEM.
[b]All females ovulated after 3 wk of LHRH-A treatment.

However, D-Trp^{6}EA-LHRH treatment accelerated ovulation in experimental females which all ovulated sometime during the final 2 wk of the experimental period.

Plasma and pituitary GtH levels were again examined. In both males and females pituitary GtH was significantly increased by LHRH analogue administration (pituitary GtH in LHRH analogue pellet group > sham controls, $P < 0.05$). D-Trp^{6}EA-LHRH stimulated GtH release in males and females for the duration of the experiment. Plasma GtH values in both sexes at 3 wk exceeded the 1-wk GtH values (plasma GtH value at 3 wk > 1 wk, $P < 0.05$).

EXPERIMENT 4 — PRESPAWNING FEMALE SALMON (TABLE 4)

Another experiment was conducted to test the effects of D-Trp^{6}EA-LHRH in prespawning females beginning in October. A GSI value approaching 20% in initial control females suggested that the vitellogenic phase was nearly completed at this time. During the 40-d-experimental period two sham control females ovulated after 29 and 30 d, respectively. D-Trp^{6}EA-LHRH advanced ovulation in the hormone-treated group. The first female ovulated on day 7 following D-Trp^{6}EA-LHRH implantation, and all females in this group were ovulated by day 12. The plasma GtH profile obtained from the blood samples collected on days 7 and 12 indicated that D-Trp^{6}EA-LHRH produces a sustained release of GtH resulting in ovulation of mature females.

EXPERIMENT 5 — SPERMIATING MALE SALMON (TABLE 5)

The influence of LHRH-A in spermiating males was investigated in January. D-Nal(2)^6-LHRH increased milt volume and also extended the duration of the spermiation period. D-Nal(2)^6-LHRH treatment did not change the relatively high GtH level (micrograms) found in the pituitaries of mature males. Plasma GtH in spermiating sham control males was consistently low; D-Nal(2)^6-LHRH stimulated GtH release throughout the 4-wk-experimental period although the highest plasma GtH values were observed in samples collected at 2-wk (plasma GtH value at 2-wk > 4-wk, $P < 0.01$).

Discussion

A clear demonstration of the effectiveness of LHRH-A treatment on GtH secretion in the landlocked salmon was provided by the present series of experiments. Evidence that LHRH or LHRH-A stimulates GtH secretion in sexually mature teleost fishes has been presented previously for carp (Breton and Weil 1973; Weil et al. 1975, 1980), trout (Crim

and Cluett 1974; Crim et al. 1981b; Weil et al. 1978), and goldfish (*Carassius auratus*) (Crim et al. 1976; Peter 1980). The results of some studies (Crim and Cluett 1974; Weil et al. 1975, 1978) suggest that the teleost pituitary undergoes seasonal changes in LHRH sensitivity but LHRH-A treatment of the landlocked salmon stimulated release of GtH throughout the year at various phases of the reproductive cycle. LHRH stimulation of GtH release from the fish pituitary gland is also supported by histological evidence of structural changes in pituitary gonadotrophs. Investigators have recorded a loss of granulation and/or a reduction in stainability of pituitary gonadotrophs following LHRH administration in the ayu (Hirose and Ishida 1974), goldfish (Kaul and Vollrath 1974; Lam et al. 1976), grass carp (*Ctenopharyngodon idella*) (Anon. 1978a, b), Atlantic salmon (Ekengren et al. 1978), and in sailfin molly (*Poecilia latipinna*) (Young and Ball 1980).

LHRH may also play a role in stimulating synthesis of GtH in the fish pituitary gland. Fang et al. (1981) noted nucleoplasmic changes in basophilic cells of the *Tilapia* pituitary following LHRH-A treatment, which were interpreted to signify the stimulation of GtH synthesis. In the landlocked salmon LHRH-A administration resulted in marked increases in pituitary GtH content of fish in the regressed or early phases of gonadal recrudescence. In more mature salmon when pituitary GtH content is already elevated, no augmentation of pituitary GtH in response to LHRH-A treatment could be demonstrated. These results suggest LHRH agonists can influence synthesis of pituitary GtH especially during the period of the seasonal reproductive cycle when pituitary GtH levels are very low. Whether LHRH-A directly affects pituitary GtH synthesis, or whether the rise in pituitary GtH content results indirectly from changing gonadal steroid feedback (Crim and Peter 1978; Crim and Evans 1979; Crim et al. 1981a), is presently unknown.

To date, many investigators have used LHRH or LHRH agonists in efforts to bring fish into breeding condition, and the biological effects upon fish gonads have been described. LHRH and LHRH-A have been used to induce maturation and ovulation in carp and other farm fishes in China (Anon. 1975, 1977a, b). LHRH evoked oocyte maturation in the European carp (Sokolowska et al. 1978; Weil et al. 1980). High doses of LHRH also induced ovulation in goldfish (Lam et al. 1975, 1976), the ayu (Hirose and Ishida 1974), and in the plaice and goby (Aida et al. 1978). The present work shows that LHRH agonists also stimulate spermiation and ovulation in landlocked salmon. Ovulation could be advanced as much as 2 mo, but when female salmon were treated with LHRH analogue beginning in October (~1 mo before spawning), ovulation was advanced and synchronized as eggs could be stripped from all females between 7 and 12 d. Recently, Donaldson et al. (1981) and Sower et al. (1982) reported that ovulation in coho salmon could be accelerated following a combination hormone treatment composed of GtH priming and then LHRH-A.

The method of administering LHRH agonists seems to play an important role in the results obtainable with these hormones. Based upon single injections of LHRH in saline (acute treatment), mature carp and trout responded to LHRH treatment, but no consistent GtH release was observed in sexually regressed animals (Crim and Cluett 1974; Weil et al. 1975; Weil et al. 1978). Frequent LHRH injections in saline promoted vitellogenesis in the medaka (*Oryzias latipes*) (Chan 1977), but when vitellogenic female brown trout (*Salmo trutta*) received multiple injections of LHRH in gelatin, no stimulation of reproductive events was recorded (Crim and Idler 1978). Compared with the saline vehicle, adjuvant emulsions of LHRH were more effective in inducing breeding in plaice and the goby (Aida et al. 1978). In contrast, olive oil emulsions of D-Trp^{6}EA-LHRH failed to induce spawning in prespawning northern pike (*Esox lucius*) (Billard and Marcel 1980). The potential advantages of formulating LHRH for slow release of the peptide hormone were recognized by Kent et al. (1980), who described a cholesterol matrix pellet formulation. LHRH-A administered in this manner to mammals prolongs biological activity for periods of several weeks. The present study represents the first opportunity to use this type of long-acting LHRH-A preparation for the purpose of manipulating the teleost reproductive cycle. In the landlocked salmon the pelleted LHRH analogues stimulated chronic GtH release lasting for periods up to 4 wk. Plasma GtH responses were elicited in recrudescent and prespawning salmon as well as in males during the sexually regressed phase of the reproductive cycle. Observing GtH release in a sexually regressed fish seems to contradict results of previous studies (cited above) indicating the presence of seasonal fluctuations in pituitary sensitivity to LHRH, but the explanation may be a matter of relative pituitary sensitivity to chronic rather than acute LHRH treatment.

TABLE 4. Influence of D-Trp^{6}EA-LHRH treatment on plasma gonadotropin and ovulation in the mature landlocked salmon (October–November).[a]

Treatment	*N*	GSI (%)	Plasma GtH, ng/mL	
			Day 7	Day 12
Initial control	3	19.4±2.2	(2.1±0.1)	
Sham control	5	[b]	2.5±0.3	2.9±0.5
LHRH-A pellet	5	[b]	34.1±7.6	41.8±3.3

[a]Values are $\bar{x}$ ± SEM.

[b]All LHRH-A-treated fish ovulated between days 7 and 12; two sham control fish ovulated (days 29 and 30, respectively). The final ovulation rate in sham controls by day 40 was 50%.

The effects of LHRH-A stimulation of prolonged elevations of plasma GtH on gonad function in fish are presently poorly understood. In August, during the rapid phase of gonadal recrudescence, male and female landlocked salmon responded quite differently to the chronic hormone changes. Vitellogenic development of females was accelerated but did not result in ovulation. In males LHRH-A treatment inhibited gonadal growth and the GSI was reduced. Evidence of testicular inhibition should perhaps be viewed with concern as chronic LHRH-A treatment causes antireproductive effects in male mammals reducing sperm production and lowering fertility (Vickery 1981). The antireproductive responses of mammals to LHRH-A treatment, the so-called paradoxical effects of LHRH, are not necessarily the result of only pituitary failure, as direct effects of LHRH upon steroidogenesis and gonadal function have also been recorded (Hsueh and Jones 1981). LHRH-A administration to the landlocked

TABLE 5. Influence of D-Nal(2)^6-LHRH treatment on plasma and pituitary gonadotropin in mature male landlocked salmon (January–February).[a]

Treatment	N	Plasma GtH, ng/mL			Pituitary GtH, μg
		Initial	2 wk	4 wk	
Sham control	4	0.82±0.09	0.83±0.18	0.61±0.04	2.57±0.6
LHRH-A pellet	5	0.80±0.04	11.7±1.79	2.33±0.52	2.14±0.3

[a]Values are $\bar{x}$ ± SEM.

salmon produced extended periods of elevated GtH, and thus there is no evidence of pituitary failure in these fish, nor is there evidence of pituitary self-suppression as described in male goldfish following multiple injections of LHRH or LHRH-A (Peter 1980). Our observations concerning the effectiveness of LHRH-A on GtH release throughout the seasonal cycle of landlocked salmon suggest that the paradoxical effects of LHRH in fish, if they exist, may be limited to specific phases of the reproductive cycle, or LHRH treatment may have direct testicular effects independent of the influence upon the pituitary gland itself.

The practice of using LHRH analogues has increased with successful demonstrations that these hormones are effective in fish for advancing spawning. Improvements in the formulations of LHRH analogues (e.g. pelleted preparations), which maximize the biological effectiveness of such hormone substances, will expand this methodology to manipulation of fish reproductive events in addition to spawning. Further studies will be required to evaluate the potential of LHRH analogues to accelerate and synchronize egg production and to stimulate the onset of sexual development in juvenile fishes or in sexually regressed adults.

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AIDA, K., R. S. IZUMO, H. SATOH, AND T. HIBIYA. 1978. Induction of ovulation in plaice and goby with synthetic LH releasing hormone. Bull. Jpn. Soc. Sci. Fish. 44: 445–450.

ANON. (CONFERENCE ON APPLICATION OF HORMONES TO ECONOMIC FISH). 1975. Kexue Tongbao 20: 43–48. (FMS Translation Series No. 4186)

(THE FUKIEN–KIANGSU–CHEKIANG–SHANGHAI COOPERATIVE GROUP FOR ARTIFICIAL REPRODUCTION OF FRESHWATER ECONOMIC FISHES). 1977a. A further investigation on the stimulatory effect of a synthetic analogue of hypothalamic luteinizing hormone releasing hormone (LRH-A) on spawning in 'Domestic Fishes.' Acta Biochim. Biophys. Sin. 9: 12–25.

(COOPERATIVE TEAM FOR HORMONAL APPLICATION IN PISCICULTURE). 1977b. A new highly effective ovulating agent for fish reproduction. Practical application of LH–RH analogue for the induction of spawning of farm fishes. Sci. Sin. 20: 469–474.

1978a. The role of LH–RH in induction of spawning in grass carp (*Ctenopharyngoden idellus*): I. Cytological and histochemical studies of the pituitary and ovary. Sci. Sin. 21: 390–396.

1978b. The role of LH–RH in induction of spawning in grass carp (*Ctenopharyngoden idellus*): II. Ultrastructural study of pituitary gonadotrophs. Sci. Sin. 21: 397–400.

BILLARD, R., AND J. MARCEL. 1980. Stimulation of spermiation and induction of ovulation in pike (*Esox lucius*). Aquaculture 21: 181–195.

BRETON, B., AND C. WEIL. 1973. Endocrinologie comparée — effets du LH/FSH–RH synthétique et d'extraits hypothalamiques de carpe sur la sécrétion d'hormone gonadotrope *in vivo* chez la carpe (*Cyprinus carpio* L.). C. R. Acad. Sci. Paris 277: 2061–2064.

CHAN, K. S. K. 1977. Effect of synthetic luteinizing hormone–releasing hormone (LH–RH) on ovarian development in Japanese medaka, *Oryzias latipes*. Can. J. Zool. 55: 155–160.

CRIM, L. W., AND D. M. CLUETT. 1974. Elevation of plasma gonadotropin concentration in response to mammalian gonadotropin releasing hormone (GRH) treatment of the male brown trout as determined by radioimmunoassay. Endocrinol. Res. Commun. 1: 101–110.

CRIM, L. W., AND D. M. EVANS. 1979. Stimulation of pituitary gonadotropin by testosterone in juvenile rainbow trout (*Salmo gairdneri*). Gen. Comp. Endocrinol. 37: 192–196.

CRIM, L. W., D. M. EVANS, D. H. COY, AND A. V. SCHALLY. 1981b. Control of gonadotropic hormone release in trout: influence of synthetic LH–RH and LH–RH analogues *in vivo* and *in vitro*. Life Sci. 28: 129–135.

CRIM, L. W., AND D. R. IDLER. 1978. Plasma gonadotropin, estradiol, and vitellogenin and gonad phosvitin levels in relation to the seasonal reproductive cycles of female brown trout. Ann. Biol. Anim. Biochim. Biophys. 18: 1001–1005.

CRIM, L. W., AND R. E. PETER. 1978. The influence of testosterone implantation in the brain and pituitary on pituitary gonadotropin levels in Atlantic salmon parr. Ann. Biol. Anim. Biochim. Biophys. 18: 689–694.

CRIM, L. W., R. E. PETER, AND R. BILLARD. 1976. Stimulation of gonadotropin secretion by intraventricular injection of hypothalamic extracts in the goldfish, *Carassius auratus*. Gen. Comp. Endocrinol. 30: 77–82.

1981a. Onset of gonadotropic hormone accumulation in the immature trout pituitary gland in response to estrogen or aromatizable androgen steroid hormones. Gen. Comp. Endocrinol. 44: 374–381.

CRIM, L. W., E. G. WATTS, AND D. M. EVANS. 1975. The plasma gonadotropin profile during sexual maturation in a variety of salmonid fishes. Gen. Comp. Endocrinol. 27: 62–70.

DONALDSON, E. M., G. A. HUNTER, AND H. M. DYE. 1981. Induced ovulation in coho salmon (*Oncorhynchus kisutch*). II. Preliminary study of the use of LH–RH and two high potency LH–RH analogues. Aquaculture 26: 129–141.

EKENGREN, B., J. PEUTE, AND G. FRIDBERG. 1978. Gonadotropic cells in the Atlantic salmon, *Salmo salar*. An experimental immunocytological, electron microscopical study. Cell Tissue Res. 191: 187–203.

FANG, Y., M. WANG, AND R. XU. 1981. The mechanisms of hypo-

thalamic luteinizing hormone releasing hormone the analogues (LHR-A): I. A study of histophysiology of pituitary gland. Acta Zool. Sin. 27: 203–210.

HIROSE, K., AND R. ISHIDA. 1974. Induction of ovulation in the ayu, *Plecoglossus altivelis* and LH-releasing hormone (LH–RH). Bull. Jpn. Soc. Sci. Fish. 40: 1235–1240.

HSUEH, A. J. W., AND P. B. C. JONES. 1981. Extrapituitary actions of gonadotropin-releasing hormone. Endocrinol. Rev. 2: 437–461.

KAUL, S., AND L. VOLLRATH. 1974. The goldfish pituitary. I. Cytologie. Cell Tissue Res. 154: 211–230.

KENT, J. S., B. H. VICKERY, AND G. I. MCRAE. 1980. The use of a cholesterol matrix pellet implant for early studies on the prolonged release in animals of agonist analogues of luteinizing hormone releasing hormone. 7th Int. Symp. on Controlled Release of Bioactive Materials. Fort Lauderdale, FL.

LAM, T. J. 1982. Applications of endocrinology to fish culture. Can. J. Fish. Aquat. Sci. 39: 111–137.

LAM, T. J., S. PANDEY, AND W. S. HOAR. 1975. Induction of ovulation in goldfish by synthetic luteinizing hormone–releasing hormone (LH–RH). Can. J. Zool. 53: 1189–1192.

LAM, T. J., S. PANDEY, Y. NAGAHAMA, AND W. S. HOAR. 1976. Effect of synthetic luteinizing hormone–releasing hormone (LH–RH) on ovulation and pituitary cytology of the goldfish *Carassius auratus*. Can. J. Zool. 54: 816–824.

NESTOR, J. J. JR., T. L. HO, R. A. SIMPSON, B. L. HORNER, G. H. JONES, G. I. MCRAE, AND B. H. VICKERY. 1982. Synthesis and biological activity of some very hydrophobic superagonist analogues of luteinizing hormone releasing hormone. J. Med. Chem. 25: 795–801.

PETER, R. E. 1980. Serum gonadotropin levels in mature male goldfish in response to luteinizing hormone–releasing hormone (LH–RH) and desGly^{10}-(D-Ala^{6})-LH–RH ethylamide. Can. J. Zool. 58: 1100–1104.

SOKOLOWSKA, M., W. POPEK, AND K. BIENIARZ. 1978. Synthetic releasing hormones LH/FSH–RH and LH–RH: effect of intracerebral and intramuscular injections on female carp (*Cyprinus carpio* L.) maturation. Ann. Biol. Anim. Biochim. Biophys. 18: 963–975.

SOWER, S. A., C. B. SCHRECK, AND E. M. DONALDSON. 1982. Hormone-induced ovulation of coho salmon (*Oncorhynchus kisutch*) held in seawater and fresh water. Can. J. Fish. Aquat. Sci. 39: 627–632.

VICKERY, B. H. 1981. Physiology and antifertility effects of LHRH and agonistic analogs in male animals, p. 275–290. *In* G. I. Zatuchni, J. D. Shelton, and J. J. Sciarra [ed.] LHRH peptides as female and male contraceptives. Harper and Row, Philadelphia, PA.

WEIL, C., R. BILLARD, B. BRETON, AND B. JALABERT. 1978. Pituitary response to LH–RH at different stages of gametogenesis in the rainbow trout (*Salmo gairdneri*). Ann. Biol. Anim. Biochim. Biophys. 18: 863–869.

WEIL, C., B. BRETON, AND P. REINAUD. 1975. Etude de la réponse hypophysaire à l'administration de Gn–RH exogène au cours du cycle reproducteur annuel chez la carpe *Cyprinus carpio* L. C. R. Acad. Sci. 280D: 2469–2472.

WEIL, C., A. FOSTIER, L. HORVATH, S. MARLOT, AND M. BERSCENYL. 1980. Profiles of plasma gonadotropin and 17β-estradiol in the common carp, *Cyprinus carpio* L., as related to spawning induced by hypophysation or LH–RH treatment. Reprod. Nutr. Dev. 20: 1041–1050.

YOUNG, G., AND J. N. BALL. 1980. Effects of LH–RH on the ultrastructure of the gonadotrophic cells of the pituitary of *Poecilia latipinna* (Teleostei) *in vivo* and *in vitro*. Gen. Comp. Endocrinol. 40: 341–342. (Abstr.)

Behavior of Crayfish in Water Currents: Hydrodynamics of Eight Species with Reference to Their Distribution Patterns in Southern Ontario

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MAUDE, S. H., AND D. D. WILLIAMS. 1983. Behavior of crayfish in water currents: hydrodynamics of eight species with reference to their distribution patterns in southern Ontario. Can. J. Fish. Aquat. Sci. 40: 68–77.

When exposed to increases in current speed in a laboratory stream tank, crayfish altered their body posture to counteract the effects of drag, thus enabling them to maintain station at higher current speeds. Using a beam-type drag balance, direct drag measurements were made on live adults of eight Ontario crayfish species over a range of current speeds. The species were then ranked according to their relative streamlining efficiencies as indexed by these drag measurement data. The station-holding abilities of the species were compared by determining the mean slip speed of each species on a roughened Plexiglas substrate. There were significant differences in slip speed, the species falling into three groups. The first contained only *Cambarus robustus*, which had a mean slip speed of 49.7 $cm \cdot s^{-1}$. The fast-water species, *Orconectes rusticus*, *C. bartoni*, and *O. propinquus*, all had mean slip speeds between 30 and 40 $cm \cdot s^{-1}$. The remaining species, *O. obscurus*, *O. virilis*, *C. fodiens*, and *O. immunis* had mean slip speeds of less than 30 $cm \cdot s^{-1}$. The crayfish species' substrate texture preferences were also tested. *Cambarus bartoni* was the only species which preferred a gravel to a mud substrate. *Orconectes obscurus*, *O. virilis*, *C. fodiens*, and *O. immunis* all preferred a mud substrate. We suggest that the superior streamlining capabilities of *C. bartoni* and *O. rusticus* may help to explain the occurrence of these species in fast-flowing rivers, as well as the latter's rapid and widespread expansion in Ontario since its introduction. On the basis of relative station-holding abilities, *O. rusticus* should continue to be more successful at expanding its range in southern Ontario via lotic waterways than the other introduced species, *O. obscurus*.

Key words: crayfish, drag, station-holding ability, streamlining, drag coefficient, hydrodynamics, posture, slip speed, substrate, distribution

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Quand elles sont exposées à des augmentations de courant dans un fluviarium, les écrevisses changent de posture afin de contrebalancer l'incidence de l'entraînement, ce qui leur permet de rester sur place. On a mesuré la résistance à l'entraînement en présence de courants variables à l'aide d'une balance à fléau chez des adultes de huit espèces d'écrevisses de l'Ontario. Les espèces ont ensuite été classées d'après l'efficacité relative de leur carénage en fonction des données de quantification de la résistance à l'entraînement. La capacité de fixation des espèces a été comparée en déterminant la vitesse moyenne de l'entraînement de chaque espèce sur un substrat de plexiglas dépoli. D'après les différences significatives de la vitesse d'entraînement, les espèces ont été réparties en trois groupes. *Cambarus robustus*, avec une vitesse moyenne d'entraînement de 49,7 $cm \cdot s^{-1}$, constitue le premier groupe. Les espèces vivant en eau vive, *Orconectes rusticus*, *C. bartoni* et *O. propinquus*, possèdent toutes une vitesse moyenne d'entraînement variant de 30 à 40 $cm \cdot s^{-1}$. Les autres espèces, soit *O. obscurus*, *O. virilis*, *C. fodiens* et *O. immunis*, ont une vitesse moyenne d'entraînement inférieure à 30 $cm \cdot s^{-1}$. La préférence de substrat de chaque espèce a aussi été étudiée. *Cambarus bartoni* est la seule espèce qui préfère un substrat gravelleux à un substrat vaseux. *Orconectes obscurus*, *O. virilis*, *C. fodiens* et *O. immunis* aiment mieux un substrat vaseux. Nous formulons l'hypothèse que le carénage plus prononcé de *C. bartoni* et

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O. rusticus aide à expliquer la présence de ces espèces dans les rivières agitées ainsi que la dissémination rapide de cette dernière espèce depuis son introduction en Ontario. À cause de sa capacité relative de fixation, *O. rusticus* devrait continuer d'avoir plus de succès de dissémination dans le sud de l'Ontario par voie des cours d'eau lotiques que l'autre espèce introduite, *O. obscurus*.

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CRAYFISH species differ in their ability to deal with water currents, and these differences are important in terms of habitat choice and species distributions (Bovbjerg 1952, 1970; Caine 1978). Mechanisms which would facilitate controlled movements through flowing water would seem to be of great importance. In terms of morphology, Alexander (1971) hypothesized that the sprawling posture of the crayfish walking legs was an adaptation to withstand overturning in strong lateral water currents. To date, the behavioral reactions of crayfish to currents of water have been little studied. Research with crayfish hydrodynamics has dealt primarily with escape responses (Webb 1979), and studies of the hydrodynamics of the directed movement of crayfish have been limited by methodology. Pond (1975), for example, used a strain gauge to measure the drag forces on crayfish corpses pulled through a tow tank at speeds up to 35 $cm \cdot s^{-1}$. To study forward motion, each corpse was fixed in a normal walking posture by inserting stiff wires into the body. However, the normal behavior of live crayfish when exposed to a current of water cannot be considered when measuring the drag forces on dead individuals. A more accurate method would be to measure drag directly on a live crayfish, so that any changes in body posture which occur in response to current would be accounted for. In addition, methods for measuring the drag on crayfish must take into consideration their benthic nature; therefore, a technique in which the crayfish are suspended in the water column is inappropriate.

Water current may affect crayfish indirectly as well, as it determines stream substrate types (Hynes 1970). Because swift streams are rocky, and sluggish streams generally have sandy or mucky bottoms, the preference for a hard substrate by fast-water species may deter them from invading slower streams, even though, in terms of current tolerance, there is no obstacle to their invasion of these habitats.

There are nine major crayfish species in Ontario, two of which are introduced (Crocker and Barr 1968). With the exception of *Cambarus diogenes* Girard, all of the species are capable of living in running water for at least part of their lives (Williams et al. 1974). The significance of rivers and streams as dispersal routes is evident from the rapid and widespread expansion of introduced species, for example, *Orconectes rusticus* (Girard) in the Kawartha Lakes region (Berrill 1978).

With the species available in southern Ontario, there exists an ideal situation for a comparative study of crayfish hydrodynamics. The objectives of this study were as follows:

1) To observe the general behavior of crayfish in response to water currents;

2) To test the relative abilities of the Ontario crayfish to maintain station in a laboratory stream tank when exposed to increases in current speed;

3) To test experimentally species' substrate preferences;

4) To develop a technique to measure directly drag forces on live crayfish and to use it to compare species' hydrodynamics;

5) To examine the data obtained with reference to the distribution patterns of the species observed in southern Ontario at present.

Materials and Methods

COLLECTION

With the exception of *C. diogenes*, which has only a marginal distribution in Ontario (Crocker and Barr 1968), adult crayfish of each species were collected between May, 1980 and October, 1981. All crayfish were caught individually by hand or dip-net. Upon return to the laboratory, crayfish were held in large, flow-through tanks for several days prior to the experiments.

GENERAL BEHAVIOR

To observe their behavior in water currents, we placed crayfish individually in a recirculating stream tank. The tank consisted of a straight channel 180 cm long by 14 cm wide with screened gates (mesh size = 1.5 mm) between it and adjoining inflow and outflow chambers. Three pumps in the outflow chamber recirculated the water to the inflow. Two of these pumps were fitted with valves, so that by regulating the number of pumps in operation and the discharge of each pump, the current speed could be varied from 0 to 80 $cm \cdot s^{-1}$. The water depth decreased slightly with increased current speed, although initially the channel was filled to a depth of 7.5 cm.

Because the crayfish were collected from a variety of substrate types ranging from mud to large boulders, we provided them with a roughened Plexiglas substrate, so that no one species would have the benefit of a "preferred" substrate.

For each species, intact, adult crayfish of both sexes were exposed to gradual increases in current speed, and postural changes were noted. Characteristically repeatable postures were standardized between species by comparison of line drawings and photographs. To determine the significance of the observed changes in posture in terms of their effects on water flow around the body of a crayfish, a dye (crystals of potassium permanganate) was added to the water so that the lines of water flow could be visualized. Potassium permanganate crystals have the advantage of providing a point source from which dye is continually released, as opposed to liquid dyes which are dissipated more quickly.

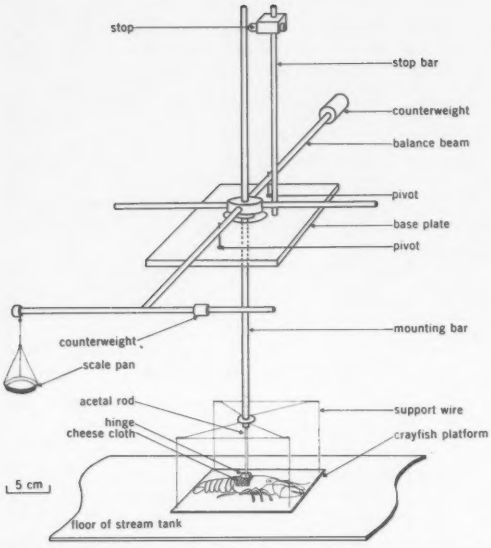

FIG. 1. Beam-type drag balance (based on Webb 1970), showing the apparatus used for attaching crayfish.

STATION-HOLDING ABILITY

Individual crayfish were selected at random and confined at the midpoint of the stream tank beneath a 30 × 14 × 7 cm bottomless Plexiglas release chamber which had numerous holes drilled in each end to allow water to flow through. Crayfish were exposed to a 15 cm · s^{-1} flow rate for 5 min. Following this the release chamber was slowly lifted out of the stream tank and the current speed was increased at a rate of 5 cm · s^{-1} · min^{-1} until the crayfish first began to slip downstream. Using a thermistor-type flowmeter (LaBarbera and Vogel 1976), this "slipspeed" (Arnold and Weihs 1978) was measured at the moment when the crayfish first lost its station. The roughened Plexiglas substrate used in the stream tank served to standardize these measurements of station-holding ability among species.

SUBSTRATE PREFERENCES

The substrate texture preferences of the crayfish species were tested in a 120 × 50 cm tank divided into two equal areas, one of soft mud and the other of coarse gravel. To minimize the number of factors involved, these preference experiments were carried out in standing water, thereby excluding the possible compounding effects of current. No large rocks were used, so that preference for a hard versus a soft substrate could be tested for, in the absence of obvious crevices in which individuals could hide. The tank was illuminated by an overhead fluorescent light on a 13:00–01:00 photoperiod. For each species, 10 crayfish were placed in the tank, and their positions were recorded twice daily, once in the light and once in the dark, for 5 consecutive days.

DRAG MEASUREMENTS

To measure the drag on live crayfish, a modified version of Webb's (1970) beam-type drag balance, designed for pelagic fishes, was used (Fig. 1). To ensure its accuracy, preliminary drag measurements were taken using flat plates and spheres for which the drag values were known (Webb 1975). Modifications of the balance included the addition of a roughened Plexiglas platform, 15 cm × 10 cm × 0.2 cm thick, to the bottom of the mounting bar, thus providing a surface on which a crayfish could stand.

A 25-mm^2 stainless-steel hinge was glued to the dorsal surface of the crayfish cephalothorax on the midline immediately posterior to the cervical groove. The surface area of the hinge proved to be too small to remain adequately adhered to the crayfish when submerged in water. It was important that this hinge be kept small, however, to minimize any disturbance it might create in the flow of water over the crayfish. To increase the effective area of contact between the hinge and the carapace, a piece of cheesecloth (14 mm × 12 mm) was soaked in adhesive and glued between the hinge and the crayfish, forming a "saddle." Crayfish were attached by this saddle to a flexible 3.2-mm-acetal rod which slid freely up and down inside the hollowed end of the mounting bar.

The design of this mounting apparatus allowed a crayfish to assume its normal postures and orientations in response to the current, because it afforded the crayfish freedom to pivot in a vertical plane, as well as the ability to raise and lower itself at will. Crayfish were placed on the platform facing upstream, and although they could turn ~45° from side to side, a set screw from the mounting bar to the acetal rod prevented them turning to face downtream. The balance apparatus was clamped on the midline of the stream tank, 110 cm downstream from the inflow gate, so that the crayfish platform was submerged to a depth of 7 cm.

At least 12 h before the experiments, crayfish were removed from the holding tanks and placed individually in 1-L-glass dishes. Immediately prior to its being mounted on the drag balance, each crayfish was removed from its dish, and its carapace was allowed to dry slightly. A "saddle" was then glued onto the carapace using a 5-min epoxy cement. Preliminary tests showed that the sequence in which an individual was exposed to the various current speeds did not affect the drag values obtained, indicating that neither fatigue nor acclimation were significant problems. Bovbjerg (1952) likewise found that crayfish did not acclimate to current. Individual crayfish remained attached to the balance for 10–20 min as the current speed was gradually increased from zero, with drag measurements being taken at speeds of 15, 25, 35, 45, and 50 cm · s^{-1}. Drag measurements were recorded only for those individuals (the majority) exhibiting streamlining behavior. The residual drag of the crayfish platform and the mounting apparatus, measured for each current speed, was subtracted from each drag measurement. Overhead red incandescent lighting was used throughout the experiments because the crayfish were least excitable when tested under these conditions. Studies of spectral sensitivity in crayfish indicate that sensitivity declines rapidly in the red wavelengths (Olivo and Chrismer 1980).

Following drag balance testing, the carapace length, total

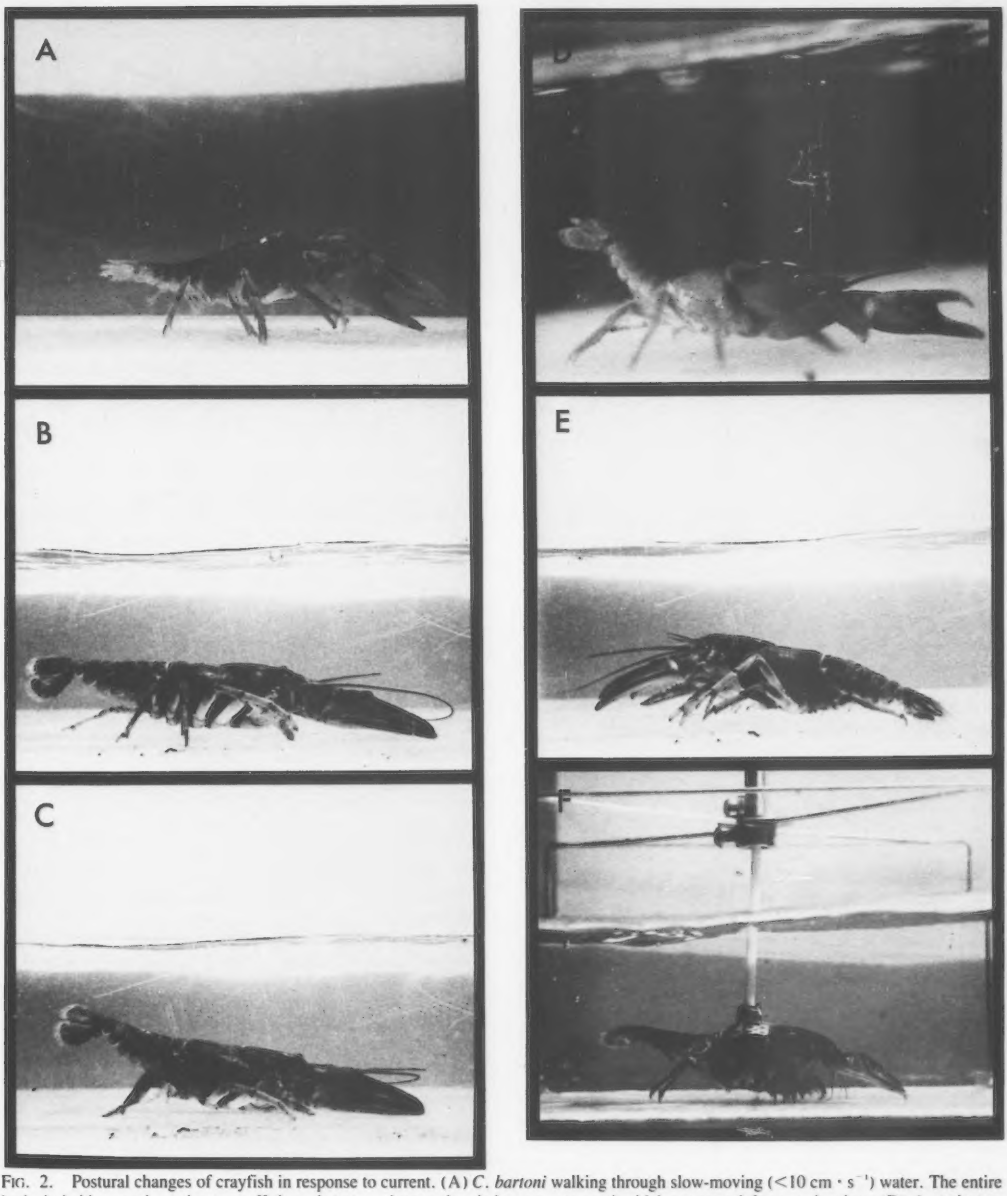

FIG. 2. Postural changes of crayfish in response to current. (A) *C. bartoni* walking through slow-moving (<10 cm · s^{-1}) water. The entire body is held several centimetres off the substrate, whereas the chelae are open and widely separated from each other. (B) A stationary *C. robustus* facing upstream in a current of ~45 cm · s^{-1}. The cephalothorax is lowered close to the substrate, the abdomen is raised only slightly, and the uropods are curved downwards. The chelae are closed and are held together in front of the head. Note also the position of the fourth pair of walking legs which are used to anchor the crayfish thus preventing it from slipping downstream. (C) *C. robustus* in the "wedge" posture, walking upstream in a current of 45 cm · s^{-1}. As in (B), the chelipeds are kept together in front of the head. In this posture the abdomen is raised higher into the water column and the anterior end is closer to the substrate, producing even more of a "plough" effect. (D) *C. bartoni* facing upstream in a current of ~40 cm · s^{-1}. The crayfish is just beginning to slip downstream. The abdomen is raised extremely high, and the right cheliped has been swept back by the current. (E) *C. robustus* walking downstream in a current of ~45 cm · s^{-1}. The uropods are pressed firmly against the substrate, preventing water flow under the crayfish body. The chelae are open and are periodically jabbed into the substrate while walking. (F) *C. fodiens* attached to the drag balance at a current speed of 45 cm · s^{-1}. Shown are the roughened Plexiglas platform, the acetal rod on the bottom of the mounting bar, and the "saddle" glued to the crayfish carapace.

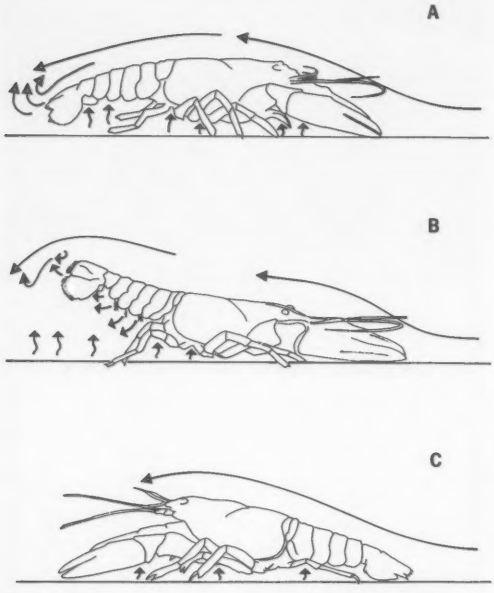

FIG. 3. Observed lines of flow around crayfish in streamlined postures. Line drawings copied from photographs; lines of flow were determined using dye visualization. (A) Stationary posture: the chelipeds are held close to the substrate to deflect the flow, so that there is virtually no flow of water under the crayfish body. (B) Wedge posture: again, the flow under the body is greatly reduced. The fanning of the pleopods produces a current of water upward onto the underside of the recurved uropods. (C) Downstream posture: the telson and uropods are pressed against the substrate, preventing water flow under the body. The great chelipeds are used to slow downstream movement.

length, and cheliped lengths of each individual were measured to the nearest 0.1 mm using vernier calipers. The height and width of the crayfish body at the insertion of the great chelipeds were measured to the nearest 0.1 mm, so that frontal areas could be estimated.

Results

GENERAL BEHAVIOR

When walking through still or slow-moving (<10 cm$\cdot$s^{-1}) water, a crayfish holds its body upright in a straight horizontal plane 1–2 cm above the substrate. Both the abdomen and the great chelipeds are usually held clear of the substrate with the latter widely separated (Fig. 2A). If the current speed is slowly increased to above 15–25 cm$\cdot$s^{-1}, crayfish will make fairly predictable behavioral changes in limb and body posture.

Specifically, a stationary crayfish facing upstream will lower its cephalothorax and abdomen to the substrate, and pull its great chelipeds together in front of the body (Fig. 2B). Flow visualization has shown that the chelipeds act as a plough, deflecting the flow of water over the top and around the sides of the crayfish. This reduces the water flow, and hence, the accompanying drag forces, on the underside of the body (Fig. 3A).

TABLE 1. The effect of streamlining behavior on station-holding ability. Results of experiments using *O. rusticus*.

Posture	Numbers of individuals exhibiting the posture	Percentage of total	Mean slip speed (cm$\cdot$s^{-1})
Upright walking posture (non-streamlined)	6	15.8	25.8
Stationary posture (streamlined)	8	21.0	52.5
Wedge posture (streamlined)	24	63.2	47.1
Total	38		Grand mean 44.9

A crayfish walking upstream in a fast current will alter its pitch by raising its abdomen high off the substrate, forming a wedge-shaped profile (Fig. 2C). The effect of this "wedge" posture is to provide a downward force on the walking legs, increasing stability for movement. As in the stationary posture, the chelipeds and cephalothorax are kept close to the substrate so that there is virtually no flow of water beneath the crayfish body (Fig. 3B).

When walking in this wedge posture, crayfish would often make fanning movements with their pleopods. This pleopod fanning produces an upward current of water on the underside of the uropods (Fig. 3B). The uropods are curved downward, forming a cup-like surface on their underside. To determine the importance of this pleopod action in stabilizing a crayfish in the current, the behavior of crayfish which had had their pleopods removed was compared with the behavior of intact individuals. There were no apparent differences; crayfish with the pleopods removed still exhibited normal reactions to current. In addition, the current speed at which individuals could no longer maintain station (Fig. 2D) was the same for each group.

The normal body posture for downstream movement in currents (Fig. 2E and 3C) is very similar to the upstream stationary posture, in that the crayfish body is held close to the substrate. The uropods are spread widely and, along with the telson, they are held down firmly onto the substrate. The tips of the great chelipeds are used as wedges; jabbed periodically into the substrate while walking, they slow movement, preventing a crayfish from sliding uncontrollably downstream.

These streamlining behavioral postures are significant because they enhance a crayfish's ability to maintain station in a current of water without slipping downstream. For example, on the average, those *O. rusticus* individuals which assumed streamlined postures could maintain station in a current speed twice that of those individuals which remained in an upright walking posture (difference between mean slip speeds, $t = 3.82$, $P < 0.001$) (Table 1).

STATION-HOLDING ABILITY

A two-factor analysis of variance indicated that there were

TABLE 2. ANOVA table for slip speed in crayfish.

Source of variation	Sum of squares	df	Mean square	F	Probability
Mean	124157.67653	1	124157.67653	922.61	<0.0001
Species	10706.82546	7	1529.54649	11.37	<0.0001
Sexual form[a]	584.10357	2	292.05178	2.17	0.12
Interaction	1945.40085	14	138.95720	1.03	0.42
Error	30951.48351	230	134.57167		

[a]Either female, male form I, or male form II. Male crayfish alternate between two distinct forms. Form I is the sexually competent form and is characterized by a more robust exoskeleton and heavier chelipeds than form II.

significant differences in slip speed among the species tested, but that intraspecific differences between the various sexual forms (male form I, male form II, female) were not significant (Table 2). The results for the three forms were therefore combined, and from these combined data a mean slip speed was calculated for each species (Table 3). These means were then compared among species using the Newman–Keuls multiple-range test (Zar 1974).

In terms of slip speed, the crayfish species fall into three main groups (Table 3). The first contains only one species, *C. robustus* (Girard), which is, on the average, able to maintain station up to a current speed of 49.7 cm · s^{-1}, significantly higher than any of the other species. The next group comprises the fast-water species, *O. rusticus*, *C. bartoni* (Fabricius), and *O. propinquus* (Girard), all of which have mean slip speeds between 30 and 40 cm · s^{-1}. These are significantly higher than the mean slip speeds of the remaining species, *O. obscurus* (Hagen), *O. virilis* (Hagen), *C. fodiens* (Cottle), and *O. immunis* (Hagen). Statistically, the group membership of *O. propinquus* is ambiguous. This is a situation which occurs fairly frequently owing to the particular procedural rules inherent in the Newman–Keuls test (Zar 1974). In this case, the result is due probably to the relatively small number of *C. fodiens* available. On the basis of field and laboratory observations of its general competence in moving through flowing water, *O. propinquus* has been included in the fast-water group.

TABLE 3. Station-holding ability of crayfish species on a roughened Plexiglas substrate. All forms combined. Numbers are the mean slip speed followed by the 95% confidence interval. Square brackets enclose those species whose means are not significantly different ($P > 0.05$) from one another based on the Newman–Keuls multiple-range test.

Species	Sample size	Range of carapace lengths (mean), in mm	Slip speed (cm · s^{-1})
C. robustus	46	32–50 (40)	49.7±4.3
O. rusticus	46	27–44 (33)	40.2±3.6
C. bartoni	42	22–32 (27)	39.0±3.9
O. propinquus	37	21–33 (25)	34.7±3.7
O. obscurus	25	23–48 (34)	29.8±3.7
O. virilis	21	27–38 (32)	28.4±5.7
C. fodiens	11	29–36 (32)	26.7±4.1
O. immunis	26	23–38 (27)	26.0±3.7

SUBSTRATE PREFERENCES

The results of the substrate preference experiments are shown in Table 4. *Orconectes virilis* and *O. immunis* both showed a decided preference for the soft, mud substrate, whereas *C. bartoni* clearly preferred the gravel. There is some indication of preference for the mud by *O. obscurus*, as well as by *C. fodiens*. When the light was on overhead, *C. fodiens* strongly preferred the mud side; however, in the dark it showed no preference for either side. It was the only species tested in which there were notable differences between the light and dark recordings.

DRAG MEASUREMENTS

The general relationship between the drag on live crayfish and current speed is shown in Fig. 4. To simplify interspecific comparisons, a least-squares regression was performed for each species on log-transformed data (Table 5). Because the crayfish were free to behave normally when on the drag balance, the degree to which the measured drag force increases with an increase in current speed [i.e. the slope of the regression line for log (drag) versus log (speed)] can serve as a measure of the ability of a species to streamline using behavioral changes in posture. For example, a species which has a small increase in drag with increases in current speed (i.e. a small slope) is more efficient at streamlining than is a species which shows large drag increases with current speed. The slopes of the regression lines (Table 5) were compared among species using the Newman–Keuls multiple-range test (Zar 1974). With the exceptions of *C. fodiens* and *O. rusticus* ($q = 0.184$, df = 574, $P > 0.50$), and *O. obscurus* and *O. propinquus* ($q = 0.0153$, df = 574, $P > 0.50$), the slopes of the regression lines were significantly different among species ($P < 0.05$).

Differences in the elevations of lines are primarily attributable to variation in size among the species, larger individuals having higher drag (Fig. 5). Even within species, males typically had greater drag than females, due to the proportionately larger size of the males' chelae.

MORPHOLOGY AND GEOMETRICAL SIMILARITY

The inherent shape of the crayfish body may limit the extent to which drag can be reduced by behavioral streamlining (Alexander 1967). Each individual's frontal area, A, was calculated assuming an elliptical cross section. On the basis of frontal area, there is an approximate geometrical similarity

TABLE 4. Substrate preferences of crayfish. Values shown refer to the number of individuals found on that substrate. Chi-square values (χ^2) were calculated for light and dark recordings combined, on the basis of random distribution. Discrepancies in sample size are due to mortality of some individuals.

Species	Light		Dark		Total		χ^2
	Mud	Gravel	Mud	Gravel	Mud	Gravel	
C. robustus	30	20	27	23	53	47	0.25 ($P>0.5$)
O. rusticus	30	19	25	24	55	43	1.23 ($P>0.1$)
C. bartoni	16	29	16	29	32	58	6.94 ($P<0.01$)
O. propinquus	29	21	25	25	54	46	0.49 ($P>0.1$)
O. obscurus	30	16	25	21	55	37	3.14 ($0.05<P<0.1$)
O. virilis	36	14	32	18	68	32	12.25 ($P<0.005$)
C. fodiens	27	12	21	20	48	32	2.81 ($0.05<P<0.1$)
O. immunis	28	12	28	12	56	24	12.01 ($P<0.005$)

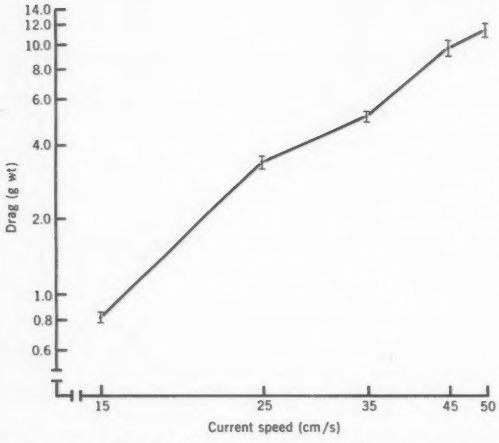

FIG. 4. An example of drag measurement data. Shown is the hydrodynamic drag on a live *O. propinquus* male (carapace length 32 mm) plotted on a logarithmic scale. Each point is the mean of 10 measurements, and the 95% confidence intervals are shown.

between all the species (Fig. 6), with A proportional to carapace length, L, according to $A \propto L^{2.15}$. This is close to $A \propto L^2$ which would be expected if there was exact geometrical similarity (Nachtigall 1977). If, however, carapace height is plotted against carapace width, some morphological differences emerge (Fig. 7). The burrowing species, *C. fodiens*, although similar in frontal area, differs from the other species in that its body is laterally compressed, the cephalothorax being higher than it is wide. In contrast, the cephalothorax of *O. immunis* is cylindrical, whereas in all the other species, it is flattened dorsoventrally.

Discussion

The results of our study clearly indicate that there are significant differences both in streamlining and station-holding abilities among the Ontario crayfish species. These differences are no doubt important ecologically, both in terms of habitat choice and species distributions. To examine the possible reasons for species differences in streamlining ability, we must first consider the general equation for hydrodynamic drag, D:

TABLE 5. Least squares regression equations for drag, D, versus current speed, U for the Ontario crayfish species. The equations are of the form: $\log D$ = (intercept) + (slope) $\log U$. (*$P < 0.001$ for all correlation coefficients.)

Species	Regression equation	Correlation coefficient*	df
C. bartoni	$\log D = -2.38 + 1.75 \log U$	0.91	103
O. rusticus	$\log D = -2.42 + 1.90 \log U$	0.85	103
C. fodiens	$\log D = -2.44 + 1.90 \log U$	0.94	48
O. immunis	$\log D = -2.56 + 2.04 \log U$	0.90	18
O. virilis	$\log D = -2.79 + 2.16 \log U$	0.94	63
O. obscurus	$\log D = -3.06 + 2.34 \log U$	0.86	78
O. propinquus	$\log D = -3.19 + 2.36 \log U$	0.95	73
C. robustus	$\log D = -3.21 + 2.58 \log U$	0.89	88

$$D = 0.5\, p\, A\, U^2\, C_D$$

where p is the density of the water, A is the frontal area of the object, U is the relative current speed, and C_D is the drag coefficient (Alexander 1968). The drag coefficient is a dimensionless number which depends on the shape of the object and the pattern of flow around it. It is not always the same for an animal moving in a given direction, as the drag coefficient may be modified by behavioral streamlining. The drag force on a body, then, may be reduced by decreasing frontal area, current speed, or the drag coefficient.

The Ontario crayfish species are very similar in terms of their frontal area (Fig. 6). Nachtigall (1977) found geometrical similarity for species of dytiscid water beetles. In the crayfish species, however, some morphological differences are apparent. In *C. fodiens* and *O. immunis*, the cephalothorax is compressed laterally compared with the other species. This is an adaptation for burrowing, as both of these species inhabit burrows for most of their life cycle (Crocker and Barr 1968; Tack 1941); a roughly cylindrical body is desirable for a burrower, because it allows the animal to escape down its burrow from any angle. Each of the other species has a cephalothorax which is dorsoventrally flattened.

Crayfish, like other inhabitants of flowing water (McCleave 1980), no doubt avoid direct exposure to currents

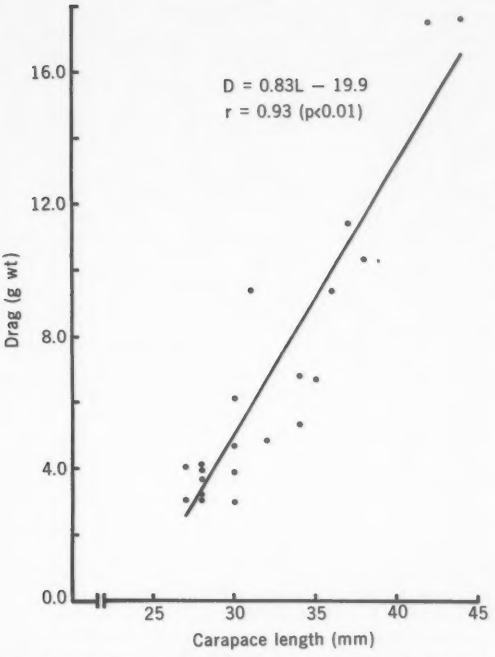

FIG. 5. An example of the relationship between size and drag. Shown is a plot of the drag D at a current speed of 50 cm · s^{-1} versus carapace length, L, in *O. rusticus*. The least squares regression line is shown.

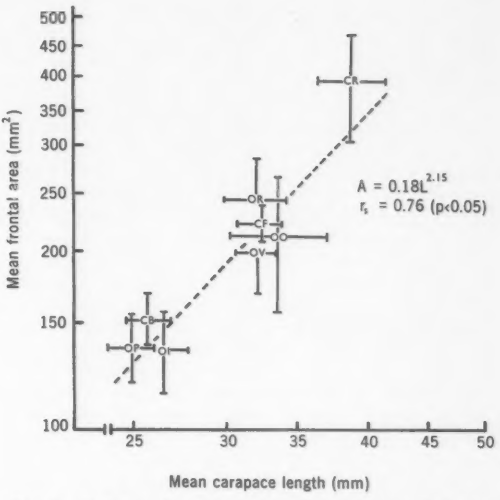

FIG. 6. Variation of frontal area, A, with carapace length, L, plotted on a logarithmic scale. Bartlett's three-group regression equation (Bartlett 1949) and the Spearman rank correlation coefficient are given. Species means and 95% confidence intervals are shown. CR, *C. robustus*; CB, *C. bartoni*; CF, *C. fodiens*; OR, *O. rusticus*; OP, *O. propinquus*; OV, *O. virilis*; OI, *O. immunis*; OO, *O. obscurus*.

by moving primarily between rocks, where the current speed is greatly reduced. However, assumptions that they are restricted to these types of movements (Pond 1975) are unrealistic.

Our observations, made in the open laboratory stream, have shown that crayfish modify their body posture when exposed to increases in current speed. In studying forward motion in crayfish, Pond (1975) studied only an upright walking posture even in current speeds of up to 35 cm·s^{-1}. By solving for the drag coefficient C_D in equation (1), we can compare our results with live crayfish to the results obtained by Pond (1975). From the data given by Pond (1975), a conservative estimate of the drag coefficient for the crayfish *Austropotamobius pallipes* (Lereboullet) is 7.6, within the range of current speeds tested. The highest drag coefficient of any crayfish in our study is substantially lower, at 5.6. The implication is that the observed postural changes reduce drag below the levels which would be expected if the crayfish always remained in their still-water walking position.

A similar example of postural changes which enhance streamlining has been reported for the benthic plaice *Pleuronectes platessa* L. (Arnold 1969; Arnold and Weihs 1978). At a threshold velocity of 1–2 cm·s^{-1}, the plaice turn to face upstream, exhibiting burying movements or a "clamped-down posture." In the clamped-down posture, the marginal fin rays are held firmly against the bottom. The streamlined posture

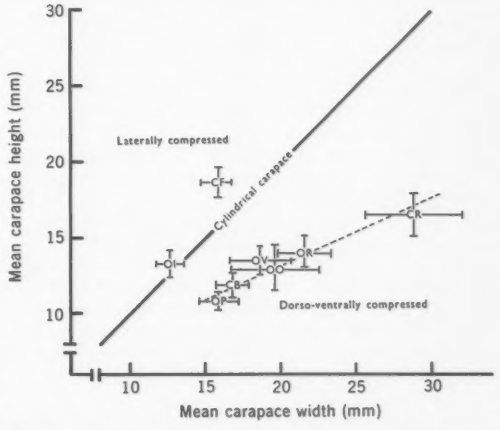

FIG. 7. Variation of carapace height with carapace width. Species means and 95% confidence intervals are shown (symbols as in Fig. 6). Species above the solid line (slope = 1) have a laterally compressed carapace; those below the line have a carapace which is compressed dorsoventrally. Bartlett's regression involving all species is not significant ($r_s = 0.24$, $P > 0.50$). However, if *C. fodiens* and *O. immunis* are excluded from the regression (broken line), there is a significant relationship ($r_s = 0.94$, $P < 0.05$).

and orientation adopted by the plaice is somewhat analogous to the stationary posture of the crayfish in which the cephalothorax and abdomen are lowered and held close to the substrate. As in the plaice, the function of the streamlining

postures in crayfish seems to be to avoid being swept downstream. When a crayfish does begin to slip downstream, it will assume the wedge posture and fan vigorously with its pleopods until it regains station.

Pleopod fanning is extremely common in crayfish. Huxley (1880) suggested that the pleopods might act as paddles, helping to propel the crayfish forwards. Removing the pleopods from crayfish, however, does not adversely affect their locomotory behavior, or their general response to water currents. In the more primitive Natantia, the pleopods are the principal swimming organs (Barnes 1980). Pleopod fanning, then, may be a primitive behavior. Its function in locomotion is not readily apparent.

The slopes of the regression lines in Table 5 can be used as an index of the relative streamlining abilities of the crayfish species: the smaller the slope, the more efficient a species is at minimizing the increases in drag due to increased current speed. In terms of body posture, there are no obvious differences between the crayfish species which could explain their relative streamlining efficiences. However, large reductions in drag could be achieved by seemingly insignificant aspects of behavior, such as slight variations in cheliped positioning. What is required is a more sensitive system whereby minute changes in body posture could be monitored to determine their immediate effects in terms of hydrodynamic drag.

The superior streamlining abilities of *C. bartoni* and *O. rusticus* may help to explain the occurrence of these species in fast-flowing rivers. Both species were collected immediately downstream from large dams where the surface velocity often exceeded 1 $m \cdot s^{-1}$, and, in fact, there is some indication that *C. bartoni* may be restricted exclusively to those areas (Berrill 1978). Also of note is the rapid and widespread expansion of the introduced *O. rusticus* (Berrill 1978), expansion which may be facilitated by its ability to cope effectively with fast-flowing water.

The good streamlining abilities of *C. fodiens* and *O. immunis* seem like anomalies. *Cambarus fodiens* is semiterrestrial, and *O. immunis* is found only in slow-water habitats. However, because these species burrow through mud, a medium significantly denser than water, streamlining is of critical importance. Efficient burrowing necessitates streamlining behavior, and thus, they are preadapted for water current. The poor station-holding abilities of these species (Table 3), and their exclusion from fast-flowing areas must be due not to a deficiency in streamlining ability, but rather to some other factor, for example, an inability to grip the substrate (Bovbjerg 1952).

The differences in the station-holding abilities of the crayfish species (Table 3) prove particularly important when examined in terms of species distributions. Those species with low slip speeds (<30 $cm \cdot s^{-1}$) — *O. immunis*, *C. fodiens*, *O. virilis*, and *O. obscurus* — are all found commonly only in slow- or still-water habitats.

Primarily a pond species, *O. immunis* is restricted in Ontario to the small ponds and low-gradient streams common in the southwest of the province. Similarly, *C. fodiens* occurs commonly only in this region. Because their tolerance to current is low, further northward expansion by *O. immunis* or *C. fodiens* seems improbable, although *C. fodiens* can migrate short distances over land (Cummins 1921). *Orconectes virilis*, although widespread in southern Ontario, is rarely found in swift creeks or rapids. Its wide distribution in the province may be due to early entry and dispersal following glaciation, as *O. virilis* is considered a long-term resident (Crocker and Barr 1968).

The ability of crayfish species to disperse via lotic waterways is particularly interesting because they are frequently introduced outside their natural ranges. For example, the introduced *O. rusticus* appears to be displacing *O. virilis* and *O. propinquus* in northern Wisconsin (Capelli and Capelli 1980). In some cases, the increased dominance of introduced species is seen as undesirable, as it often results in hybridization (Capelli and Capelli 1980; Smith 1979), and it occurs at the expense of rare, native species (Daniels 1980; Jay and Holdich 1981; Riegel 1959).

Crayfish migrations in streams have been observed in several field studies. In Michigan, stream-dwelling *O. virilis* individuals were found to undergo seasonal upstream migrations, presumably to prevent extensive displacement by downstream water movements (Hazlett et al. 1979). Similarly, Hobbs (1978) reported that the troglobitic crayfish *O. inermis testii* (Hay) moved upstream to compensate for the downstream displacement which occurred during spates. Henry (1951) recorded that *Pacifastacus klamathensis* (Stimpson) migrated downstream in the late spring and early summer, with a return migration upstream in the fall. Momot (1966) found that, in an intermittent stream, *O. nais* (Faxon) migrated extensively upstream from a silt to a rubble substrate. In the late summer and early fall, adult *O. virilis* individuals moved away from the shoal areas of a stream and into deeper, faster-flowing areas, thereby surviving severe winter conditions (Aiken 1968).

Orconectes obscurus has migrated very little since its introduction into the Kawartha Lakes region (Berrill 1978). Its natural range is also small (Crocker and Barr 1968), and this, combined with its inability to deal with the fast rivers of the Kawartha region, suggests that, barring new introductions, further expansion of its Ontario range is unlikely. In contrast, the introduced *O. rusticus* has expanded its range to the extent that now, in the Kawarthas, only *O. propinquus* is more common. Judged strictly on the basis of its station-holding ability (Table 3), this species' range expansion seems certain to continue.

In the substrate preference experiments, *C. bartoni* was the only species which clearly preferred a gravel to a mud substrate (Table 4). It was found primarily in the shallow rapids of rocky streams. Here individuals excavated and occupied shallow holes in loose gravel. McManus (1960) reported a case of burrow and chimney construction by *C. bartoni* in the exposed rubble area of a stream during a period of low water. He suggested that burrowing by this species probably also occurred in the stream, but that the overflowing water normally prevented the formation of chimneys.

All four of the slow-water species preferred the mud substrate. This is in disagreement with Bovbjerg (1970), who reported that *O. virilis* and *O. immunis* preferred a rock substrate over either gravel or muck. However, by using rocks, Bovbjerg provided potential shelters for the crayfish, so that he was no longer testing strictly a substrate texture preference.

Cambarus fodiens favored the mud substrate only in the

light; in the dark, individuals were divided equally between the mud and gravel. This may reflect the increase in activity of this species at night. These crayfish remain hidden in their burrows throughout the day; only during the night do they venture out to forage and enter open-water areas (Cummins 1921; Williams et al. 1974).

Current, then, affects the habitat choices and range limitations of crayfish both directly, in terms of station-holding, and indirectly, by influencing stream substrate types. However, there are clearly many other factors involved in the determination of species distributions. For example, in addition to current and substrate, low oxygen levels, extremes in temperature and pH, the temporary drying of streams and ponds, and interspecific aggressive encounters could all act as limiting factors for crayfish species.

Acknowledgments

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AIKEN, D. E. 1968. The crayfish *Orconectes virilis:* survival in a region with severe winter conditions. Can. J. Zool. 46: 207–211.

ALEXANDER, R. McN. 1967. Functional design in fishes. Hutchinson and Co. Ltd., London. 160 p.

1968. Animal mechanics. Univ. Wash. Press, Seattle, WA. 346 p.

1971. Size and shape. Edward Arnold, London. 59 p.

ARNOLD, G. P. 1969. The reactions of the plaice (*Pleuronectes platessa* L.) to water currents. J. Exp. Biol. 51: 681–697.

ARNOLD, G. P., AND D. WEIHS. 1978. The hydrodynamics of rheotaxis in the plaice (*Pleuronectes platessa* L.). J. Exp. Biol. 75: 147–169.

BARNES, R. D. 1980. Invertebrate zoology. 4th ed. Saunders College, Philadelphia, PA. 1089 p.

BARTLETT, M. S. 1949. Fitting a straight line when both variables are subject to error. Biometrics 5: 207–212.

BERRILL, M. 1978. Distribution and ecology of crayfish in the Kawartha Lakes region of southern Ontario. Can. J. Zool. 56: 166–177.

BOVBJERG, R. V. 1952. Comparative ecology and physiology of the crayfish, *Orconectes propinquus* and *Cambarus fodiens*. Physiol. Zool. 25: 34–56.

1970. Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). Ecology 51: 225–236.

CAINE, E. A. 1978. Comparative ecology of epigean and hypogean crayfish (Crustacea: Cambaridae) from northwestern Florida. Am. Midl. Nat. 99: 315–329.

CAPELLI, G. M., AND J. F. CAPELLI. 1980. Hybridization between crayfish of the genus *Orconectes:* morphological evidence (Decapoda: Cambaridae). Crustaceana 39: 121–132.

CROCKER, D. W., AND D. W. BARR. 1968. Handbook of the crayfishes of Ontario. University of Toronto Press, Toronto, Ont. 158 p.

CUMMINS, H. 1921. Spring migration in the crayfish, *Cambarus argillicola* Faxon. Trans. Am. Microsc. Soc. 40: 28–30.

DANIELS, R. A. 1980. Distribution and status of crayfishes in the Pit River drainage, California. Crustaceana 38: 131–138.

HAZLETT, B., D. RITTSCHOF, AND C. AMEYAW-AKUMFI. 1979. Factors affecting the daily movements of the crayfish *Orconectes virilis* (Hagen, 1870) (Decapoda, Cambaridae). Crustaceana, Suppl. (Leiden) 5: 121–130.

HENRY, K. A. 1951. Spring Creek crayfish migrations 1949 and 1950. Oregon Fish. Comm. Res. Briefs 3: 48–55.

HOBBS, H. H. 1978. Biology of the cave crayfish *Orconectes inermis testii* (Hay) (Decapoda: Cambaridae) in Indiana. Nat. Speleol. Soc. Bull. 40: 86.

HUXLEY, T. H. 1880. The crayfish; an introduction to the study of zoology. Vol. 28. The International Scientific Series, D. Appleton, New York, NY.

HYNES, H. B. N. 1970. The ecology of running waters. Liverpool University Press, Liverpool. 555 p.

JAY, D., AND D. M. HOLDICH. 1981. The distribution of the crayfish, *Austropotamobius pallipes* in British waters. Freshw. Biol. 11: 121–129.

LABARBERA, M., AND S. VOGEL. 1976. An inexpensive thermistor flowmeter for aquatic biology. Limnol. Oceanogr. 21: 750–756.

MCCLEAVE, J. D. 1980. Swimming performance of European eel (*Anguilla anguilla* (L.)) elvers. J. Fish Biol. 16: 445–452.

MCMANUS, L. R. 1960. An occurrence of "chimney" construction by the crayfish *Cambarus b. bartoni*. Ecology 41: 383–384.

MOMOT, W. T. 1966. Upstream movement of crayfish in an intermittent Oklahoma stream. Am. Midl. Nat. 75: 150–159.

NACHTIGALL, W. 1977. Swimming mechanics and energetics of locomotion of variously sized water beetles (Dytiscidae) body length 2–35 mm, p. 269–283. *In* T. J. Pedley [ed.] Scale effects in animal locomotion. Academic Press, New York, NY.

OLIVO, R. F., AND K. L. CHRISMER. 1980. Spectral sensitivity of screening-pigment migration in retinula cells of the crayfish *Procambarus*. Vision Res. 20: 385–390.

POND, C. M. 1975. The role of the 'walking legs' in aquatic and terrestrial locomotion of the crayfish *Austropotamobius pallipes* (Lereboullet). J. Exp. Biol. 62: 447–454.

RIEGEL, J. A. 1959. The systematics and distribution of crayfishes in California. Calif. Fish Game 45: 29–50.

SMITH, D. G. 1979. Variability of crayfish of the *virilis* section (Cambaridae: *Orconectes*) introduced into New England and eastern New York. Am. Midl. Nat. 102: 388–391.

TACK, P. I. 1941. The life history and ecology of the crayfish *Cambarus immunis* Hagen. Am. Midl. Nat. 25: 420–444.

WEBB, P. W. 1970. Some aspects of the energetics of swimming of fish with special reference to the cruising performance of rainbow trout. Ph.D. thesis. Univ. Bristol. Bristol, England. 189 p.

1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Board Can. 190: 159 p.

1979. Mechanics of escape responses in crayfish (*Orconectes virilis*). J. Exp. Biol. 79: 245–263.

WILLIAMS, D. D., N. E. WILLIAMS, AND H. B. N. HYNES. 1974. Observations on the life history and burrow construction of the crayfish *Cambarus fodiens* (Cottle) in a temporary stream in southern Ontario. Can. J. Zool. 52: 365–370.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc. Englewood Cliffs, NJ. 620 p.

NOTES

Relationship Between Body-Lead Concentration of *Mysis relicta* and Sediment-Lead Concentration in Kootenay Lake, B.C.[1]

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EVANS, R. D., AND D. C. LASENBY. 1983. Relationship between body-lead concentration of *Mysis relicta* and sediment-lead concentration in Kootenay Lake, B.C. Can. J. Fish. Aquat. Sci. 40: 78–81.

The potentially important mechanism of biological mobilization of lead from lake sediments was investigated. Lead concentrations of the crustacean *Mysis relicta* from Kootenay Lake, determined using atomic absorption spectrophotometry, were compared to published lead sediment concentrations from the same sites. There is a strong correlation between sediment-lead concentration and *Mysis*-lead concentration. This correlation may indicate that *Mysis* can accumulate lead from the sediment and return it to the open water.

Key words: *Mysis relicta*, lead, heavy metal contamination, contaminated sediments.

EVANS, R. D., AND D. C. LASENBY. 1983. Relationship between body-lead concentration of *Mysis relicta* and sediment-lead concentration in Kootenay Lake, B.C. Can. J. Fish. Aquat. Sci. 40: 78–81.

L'article qui suit contient les résultats d'une étude du mécanisme potentiellement important de la mobilisation biologique du plomb des sédiments lacustres. Nous avons comparé les concentrations de plomb dans le crustacé *Mysis relicta* du lac Kootenay, déterminées par spectrophotométrie à absorption atomique, avec celles du sédiment aux mêmes endroits, extraites des travaux publiés. Il y a étroite relation entre la concentration de plomb dans le sédiment et chez *Mysis*. Cette corrélation peut indiquer que ce crustacé est capable d'accumuler le plomb du sédiment et le retransmettre à la pleine eau.

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INDUSTRIAL and cultural activities in North America have led to the widespread dispersal of many substances potentially toxic to aquatic biota. Trace metals (lead, copper, zinc) and synthetic organics (PCBs, dioxin) have received considerable attention in recent years. Substantial quantities of these anthropogenic substances are ultimately deposited in lakes and rivers (Kemp et al. 1978; Wakeham 1979). This increase has been found in remote locations as well as those close to identifiable sources (Evans and Rigler 1980; Dillon and Evans 1982). Thus the recent sediments of most lakes in North America represent a large pool of potentially harmful substances. For example, Dillon and Evans (1982) have determined that, on average, the top few centimetres of sediments in all lakes in the Muskoka–Haliburton region of Ontario contain about 1 g Pb/m^2 with localized deposits being several times this amount.

Some authors have suggested that, based solely on chemical mobilization, the potential for the return of lead from the sediments to the overlying water should be small (Davis et al. 1982). Physical mobilization is probably small as well because in most lakes typical bottom currents are insufficient to remobilize sediment particles (Sly 1973; Hakanson 1977). One potentially important mechanism, however, is the biological mobilization of metals. There are many migrating benthic organisms that inhabit both the relatively uncontaminated pelagic regions as well as the contaminated sediment (e.g. *Mysis relicta*, *Pontoporia*). In addition, they serve as an important food source for higher trophic levels such as fish (Northcote 1973; Reynolds and DeGraeve 1972). The potential exists for these organisms to accumulate metals from the large pool available in the sediments and, in their daily vertical migrations, return them to the pelagic regions of a lake. If they, or their fecal pellets, are a food source for other organisms, the result may be the incorporation of contaminants such as lead into organisms that are not normally exposed to significant quantities of such substances.

[1]Contribution No. 1 of the Trent Aquatic Research Group.

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Mysis relicta is an ideal organism for transporting metals from the sediments as it is a benthic detritivore by day, vertically migrating into the open water at night to feed on plankton. Its average gut passage time is ~3–5 h (Lasenby and Langford 1973). Thus sediment ingested during the day will remain in the gut throughout most of the night when it is available as a food source to pelagic fish. This is important as the largest portion of metals in an invertebrate may be in the gut contents rather than in the animal tissue (Elwood et al. 1976). As well, *Mysis* is being introduced into hundreds of lakes in North America and Scandinavia to serve as a supplementary food source for fish (Riemen and Falter 1981; Furst et al. 1978). This study examines the relationship between sediment-lead concentration and organism-lead concentration. If migrating benthic organisms are acting as "metal pumps" to return lead to the pelagic region from the sediments, one would predict a positive correlation between sediment-lead concentration and organism-lead concentration.

Methods — Kootenay Lake, British Columbia, was chosen for this study because it has a large population of *M. relicta* (Daley et al. 1980). As well, it has been exposed to large quantities of lead, primarily from silver mines within the watershed (Daley et al. 1980). As a result there are strong gradients in lead concentration in the lake sediments with lowest concentrations at the north and south ends of the lake and highest concentrations towards the middle (Daley et al. 1980).

Mysis relicta was collected from Kootenay Lake during the summers of 1977 and 1978 at eight stations (Fig. 1) and preserved immediately in 70% alcohol. Two samples from each station were analyzed for total lead content. Each sample consisted of 150–300 animals representing the range of the individual sizes available. The mysids were dried at 80°C for at least 48 h and the dry weight of each sample recorded. The dried animals were then digested at 80°C in a 2:1 mixture of HCl (sp gr 1.18) and HNO_3 (sp gr 1.42). This method is an adaptation of that previously used to analyze lake sediments (Evans 1980). The digestate was taken to dryness and redissolved in 1.5 mol/L HCl, centrifuged, and analyzed for total lead using a Varian model AA375 atomic absorption spectrophotometer. Analysis of the alcohol before and after storage of the animals indicates that at most 3% of the lead in the animals is lost to the alcohol during storage. Because of the high organic content of aquatic invertebrates several samples were also digested using perchloric acid with no apparent differences in total lead content between the two digestion techniques. Results have been expressed as micrograms of lead per gram dry weight for both sediments and mysids.

Results and discussion — Mysids collected at two different times during the summer at each station were analyzed for lead concentration. The differences in lead concentration for a particular site ranged between 1 and 18% (Table 1). The differences between stations in lead concentration were much greater. Average whole body concentrations ranged from 1.5 to 15.0 μg/g. The concentrations of lead observed in the mysids at the lower end of this range are very similar to those observed by Whittle (I.J.C. 1980) in Lake Ontario mysids.

FIG. 1. Sample sites on Kootenay Lake. Numbers are sediment-lead concentrations (from Daley et al.) in μg/g dry weight.

In Kootenay Lake, the lead concentration of the surficial sediments varies from 35 to 750 μg/g at the stations at which *Mysis* were collected (Fig. 1). These values were estimated from Daley et al. (1980). The water flow pattern in the lake is such that any movement of mysids would be from either the north or south end to the middle of the lake and ultimately out through the west arm. As a result of the unique spatial variation in sediment-lead concentration and water movement, it is unlikely that mysids ever move from areas of high contamination in the middle of the lake to areas of low contamination at the north or south ends. If mysids do obtain lead from sediments, one would expect to find higher lead concentrations in mysids from the midlake regions than the ends of the lake.

In Table 1 the average lead concentration of the mysids from each station is compared to the surficial sediment lead concentration. There is a strong correlation between the two factors ($n = 8$, $r^2 = 0.92$, $P < 0.01$). The relationship between sediment-lead concentration and mysid-lead concentration strongly suggests that mysids can obtain lead from sediment. The discrete nature of the relationship indicates either that the mysids remain in one area of the lake for long periods of time, or that there is an immediate response of the mysids to a new habitat which is reflected in gut contents of the animals. For example, mysids in Crawford Bay exhibit low lead concentrations although found in close proximity to the contaminated sediments in the main body of the lake.

In an effort to determine at what stage in the life history sediment feeding becomes important, we measured lead concentration on three different size-classes of mysids from

TABLE 1. Lead in sediments and *Mysis* from eight stations in Kootenay Lake.

Station	Avg. wt of *Mysis* (mg dry wt)	Avg. lead concn in *Mysis* (μg/g dry wt)	Lead concn in surficial sediments[a] (μg/g dry wt)
Lardeau	7.7	2.9	35
	5.9	2.8	
Kaslo	9.0	6.2	350
	9.4	5.7	
Ainsworth	5.2	11.9	750
	5.1	14.4	
Queen's Bay	5.7	13.7	750
	5.7	15.2	
Crawford Bay	10.8	1.5	20
	10.1	1.4	
Lockhart Beach	8.3	8.5	160
	7.2	7.5	
Pilot Bay	2.0	13.5	750
	1.4	16.4	
Kushanook	13.3	3.1	75
	7.6	2.3	

[a]From Daley et al. (1980).

TABLE 2. Variation in lead concentration with *Mysis* length in Queen's Bay.

Size (mm)	Sample size (no.)	Avg. dry wt (mg)	Lead concn (μg/g dry wt)
6–8	650	0.44	12.3
11–13	300	3.07	8.9
17–20	100	6.96	14.4

contaminated Queen's Bay (6–8, 11–13, and 17–20 mm). The lead concentration per unit weight did not increase consistently throughout the life history (Table 2). In contrast, Sarkka (1979) found that immature mysids (<1 yr) contain significantly lower mercury concentrations than those over 1 yr in age. If such a trend occurs for lead as well as mercury, it may have been obscured by our size fractionation.

The correlation between mysid lead and sediment lead is not direct evidence that sediments are the only, or indeed, the major source of metal in the organism. Alternately, the migrating benthic organism may be absorbing metals from the open water overlying the sediments. However, lead concentrations in the open water are normally at or below the detection limit (Jaworski 1978) whereas sediment concentrations are up to three orders of magnitude higher (Dillon and Evans 1982). A relation between open-water and organism-lead concentrations would be extremely difficult to document, although such a relationship has been suggested by Whittle (I.J.C. 1980) for *Mysis* in Lake Ontario. Detailed laboratory studies are underway aimed at directly testing this question. However, Sarrka (1979) found that profundal invertebrates had higher concentrations of both mercury and DDT than littoral inhabitants in Lake Paijanne, Finland. Although it is unlikely that open-water concentrations vary markedly, because of turbulent mixing, it has been well documented that profundal sediments are more heavily contaminated than those in the littoral zone within a given lake (Robbins 1980; Evans and Rigler 1980). Thus the results of Sarrka's work may indicate sediment feeding and incorporation by the organisms.

Uptake of lead by other benthic organisms has been documented in experimental situations. Patrick and Loutet (1976) found uptake of lead-contaminated bacteria by tubificid worms resulting in the worms becoming equilibrated to the bacteria-lead concentration. Packer et al. (1980) found a positive correlation between sediment metal concentrations (including lead) and body concentrations in the marine polychaete *Arenicola marina* in the Bristol Channel. Although these experiments indicate a basis for the expectation of results such as ours, further studies would be useful in determining the generality of our results in terms of other benthic organisms and differing sediment concentrations.

Although there is no direct evidence that consumption of lead-contaminated mysids is leading to increased body burdens of fish in Kootenay Lake, the implications of this work are clear. Mysids have been and continue to be introduced into lakes as a food source for fishes. Principally they are used to enhance stocks of game and/or commercial fishes. In lakes in which *Mysis* has been introduced, they make up from 70 to 100% of the diet of pelagic fishes (Furst et al. 1978). In Kootenay Lake mysids comprise between 25 and 75% of the food supply of kokanee salmon (*Oncorhynchus nerka*) (Northcote 1973). For example, it has been estimated that *Mysis* and *Ponteporia*, feeding on contaminated sediments in Lake Michigan, are responsible for over 50% of the PCB burden in lake trout (Delfino 1979). If the effect of mysid introductions is to encourage the fish to move away from open water to a bottom-feeding food source, then the negative impact of increased contaminant burdens may be greater than the overall benefits of increased catches.

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CRECELIUS, E. A., AND D. Z. PIPER. 1973. Particulate lead contamination recorded in sedimentary cores from Lake Washington, Seattle. Environ. Sci. Technol. 7: 1053–1055.

DALEY, R. J., E. C. CARMACK, C. B. J. GRAY, C. H. PHARO, S. JASPER, AND R. C. WIEGAND. 1981. The effects of upstream impoundments on the limnology of Kootenay Lake, B.C. Natl Water Res. Inst. Sci. Ser. No. 117.

DAVIS, A. E., J. N. GALLOWAY, AND D. K. NORDSTROM. 1982. Lake acidification: its effect on lead in the sediment of two Adirondack Lakes. Limnol. Oceanogr. 27: 163–167.

DELFINO, J. J. 1979. Toxic substances in the Great Lakes. Environ. Sci. Technol. 13: 1462–1468.

DILLON, P. J., AND R. D. EVANS. 1982. Whole lake lead burdens in sediments of lakes in Southern Ontario, Canada. 2nd Int. Symp. on Sediment–Freshwater Interactions, Kingston, Canada, June, 1981. Hydrobiologia 91: 12.

ELWOOD, J. W., S. G. HILDEBRAND, AND J. J. BEAUCHAMP. 1976. Contribution of gut contents to the concentration and body burden of elements in *Tipula* spp. from a spring fed stream. J. Fish. Res. Board Can. 33: 1930–1938.

EVANS, R. D., AND F. H. RIGLER. 1980. Calculation of the total anthropogenic lead in the sediments of a rural Ontario lake.

Environ. Sci. Technol. 14: 216–218.
FURST, M., U. BOSTROM, AND J. HAMMAR. 1978. Effects of new fish-food organisms in Lake Blasjon. Inf. Sotvattens-Lab Drottningholm 15: 94 p.
GALLOWAY, J. N., AND G. E. LIKENS. 1979. Atmospheric enhancement of metal deposition in Adirondack Lake sediment. Limnol. Oceanogr. 24: 427–433.
HAKANSON, L. 1977. The influence of wind, fetch, and water depth on the distribution of sediments in Lake Vanern, Sweden. Can. J. Earth Sci. 14: 397–412.
I.J.C. 1980. Lead, p. 63–102. *In* Report of the Aquatic Ecosystem Objectives Committee to the Science Advisory Board. International Joint Commission, Regional Office, Windsor, Ont.
JAWORSKI, J. F. 1978. Effects of lead in the environment — 1978 Quantitative aspects. Nat. Res. Counc. Can. Assoc. Comm. Sci. Criter. Environ. Qual. Publ. 16736.
KEMP, A. L., J. D. H. WILLIAMS, R. L. THOMAS, AND M. L. GREGORY. 1978. Impact of man's activities on the chemical composition of the sediments of Lakes Superior and Huron. Water Air Soil Pollut. 10: 381–402.
LASENBY, D. C., AND R. R. LANGFORD. 1973. Feeding and assimilation of *Mysis relicta*. Limnol. Oceanogr. 18: 280–285.
NORTHCOTE, T. G. 1973. Some impacts of man on Kootenay Lake and its salmonids. Great Lakes Fish. Comm. Tech. Rep. 25.
PACKER, D. M., M. P. IRELAND, AND R. J. WOTTON. 1980. Cadmium copper, lead, zinc, and manganese in the polychaete *Arenicola marina* from sediments around the coast of Wales. Environ. Pollut. Ser. A Ecol. Biol. 22: 309–321.
PATRICK, R. M., AND M. LOUTIT. 1976. Passage of metals in effluents through bacteria to higher organisms. Water Res. 10: 333–335.
REIMAN, B. E., AND C. M. FALTER. 1981. Effects of the establishment of *Mysis relicta* on the macrozooplankton of a large lake. Trans. Am. Fish. Soc. 110: 613–620.
REYNOLDS, J. B., AND G. M. DEGRAEVE. 1972. Seasonal population characteristics of the oppossum shrimp, *Mysis relicta*, in southeastern Lake Michigan, 1971–71. Proc. 15th Conf. Great Lakes Res. 177–131.
ROBBINS, J. A. 1980. Sediments of southern Lake Huron: elemental composition and accumulation rates. EPA 600/3-80-080: 309 p.
SARRKA, J. 1979. Mercury and chlorinated hydrocarbons in zoobenthos of Lake Paijanne, Finland. Arch. Environ. Contam. Toxicol. 8: 161–173.
SLY, P. G. 1973. The significance of sediment deposits in large lakes and their energy relationships, p. 383–396. Proceedings of the Symposium of the Hydrology of Lakes (IAHS–AISH Publ. 109), Helsinki, Finland.
WAKEHAM, S. G. 1979. Azaarenes in recent lake sediments. Environ. Sci. Technol. 13: 1118–1123.

Effect of Increased Dietary Fiber on the Growth of Rainbow Trout (*Salmo gairdneri*)

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HILTON, J. W., J. L. ATKINSON, AND S. J. SLINGER. 1983. Effect of increased dietary fiber on the growth of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 40: 81 – 85.

Juvenile rainbow trout (*Salmo gairdneri*) reared for 12 wk on different levels of dietary fiber showed a significant growth depression at levels of 10 and 20% alpha-floc (α-cellulose). The trout adapted to increased dietary fiber by increasing feed consumption, gastric evacuation time, and possibly by increasing the stomach volume and/or distensibility. The dry matter digestion coefficients of the diets declined as the fiber level increased, indicating that the digestibility of α-cellulose was not significantly different from zero. No effect of increased dietary fiber (alpha-floc) was detected on the liver glycogen levels, liver–body weight ratios, hemoglobin, hematocrit, plasma glucose, and plasma protein levels or the kidney, liver, and carcass levels of copper, iron, and zinc. We conclude that dietary fiber levels for rainbow trout should be less than 10% of the diet.

Key words: rainbow trout, dietary fiber, maximum fiber level, fiber digestibility

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À des niveaux de 10 et 20 % d'alpha-floc (α-cellulose), de jeunes truites arc-en-ciel (*Salmo gairdneri*), élevées pendant 12 semaines à différents niveaux de fibres alimentaires, montrent une importante diminution de croissance. Les truites se sont adaptées à une augmentation de fibres alimentaires par un plus grand volume de nourriture consommée, par un temps d'évacuation du bol alimentaire plus long et, possiblement, par un volume et (ou) une élasticité accrus de l'estomac. Les coefficients de digestion de la matière sèche des régimes diminuent à mesure qu'augmente le niveau des fibres, signe que la digestibilité de l'α-cellulose ne diffère pas significativement de zéro. Une augmentation des fibres alimentaires (alpha-floc) n'a pas d'effet détectable sur les paramètres suivants : niveaux de

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glycogène hépatique, rapports poids du foie : poids du corps, hémoglobine, hématocrite, niveaux de glucose et de protéines plasmatiques, ou niveaux de cuivre, de fer et de zinc dans le foie et la carcasse. Nous concluons que les niveaux de fibres alimentaires de la truite arc-en-ciel devraient être inférieurs à 10 % du régime.

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THE generic name fiber refers to all indigestible plant matter such as celluloses, lignins, and other complex carbohydrates in animal diets. Natural diets of trout generally contain little dietary fiber, but commercial diets contain varying amounts of complex carbohydrates depending upon the level of inclusion of cereal meals in the feed formulation. Buhler and Halver (1961) observed depressed growth rates in chinook salmon (*Oncorhynchus tshawytscha*) reared on diets with increasing levels of α-cellulose. Although Dupree and Sneed (1966) reported growth improvement in channel catfish (*Ictalurus punctatus*) reared on purified diets with 21% cellulose, Leary and Lovell (1975) observed a growth depression using practical diets with 8% or more of cellulose. The National Research Council (1977) indicates that fiber levels of 8% or less in semipurified test diets of catfish may add structural integrity to pelleted diets and improve the growth rate of these fish. Therefore, the physiological effect of increased dietary fiber on fish are uncertain, but could conceivably have a significant effect on the growth and physiological response of fish.

This study was conducted to determine the effect of supplemental dietary fiber, as alpha-floc, on the growth and physiological response of rainbow trout (*Salmo gairdneri*).

Materials and methods — Diet formulation and maintenance of trout — Three practical trout diets were formulated with increasing dietary fiber, as alpha-floc, at levels of 0, 10, and 20% of the basal diet (Table 1), replacing the diet as a whole. The diets were processed by steam pelleting in a California pellet mill (San Francisco, CA, USA). The ash, dry matter, crude fiber, and protein ($N \times 6.25$) content of the diets were determined by the methods of Horwitz et al. (1970) and the lipid content by the method of Bligh and Dyer (1959).

Juvenile rainbow trout were obtained from the Ontario Ministry of Natural Resources, Normandale Hatchery, Turkey Point, Ont., Canada. After a 2-wk acclimation period, ~100 fish per tank (mean weight 5.3 ± 0.2 g/fish) were transferred to two 12-tank systems which were in different rooms. One system of tanks comprised rectangular fiber glass tanks (60-L capacity) and the other enamel-lined rectangular metal tanks (45-L capacity). The tanks were individually aerated, kept at 15.4 ± 0.9°C with a flow rate of 2−3 L per minute, with the oxygen concentration and pH varying between 7.7 and 9.4 mg/L and 7.3 and 7.8, respectively, throughout the study.

The test diets were fed to the trout according to two different feeding schedules (A and B). In A the ad libitum feeding level of the group fed the 0% alpha-floc diet was determined at each feeding; for the trout receiving the 10 and 20% alpha-floc diets, an attempt was then made to adjust feed intake so as to provide the same nutrient intake levels as in the no alpha-floc group. Alpha-floc was assumed to have no energy or nutrient value. In B, the ad libitum feeding level of the trout reared on the 20% alpha-floc diet was determined at each feeding. The feeding levels of the remaining two dietary groups, 0 and 10% supplemental alpha-floc, were then adjusted to provide the same nutrient levels as in the 20% alpha-floc diet. The test diets were fed to quadruplicate groups of trout for 12 wk in a split-plot design in the two 12-tank systems.

Growth and biochemical assays — Body weights, feed:gain ratios, and total mortalities were determined after each 28-d period. Feed intake for each tank was monitored and recorded for each feeding. After 12 wk, blood was collected from about eight fish (fasted 18 h) from each group, in heparinized centrifuge tubes by transection of the caudal peduncle, and immediately centrifuged at 3500 × *g* for 5 min. Plasma was then stored at −20°C until required for analysis. Plasma glucose was determined by the glucose oxidase method (Boehringer−Mannheim kit), plasma protein by the method of Lowry et al. (1951), hemoglobin by the cyanmethemoglobin method (Unopette test 587, Becton Dickinson Co. Ltd., Mississauga, Ont., Canada), and hematocrit using microhematocrit tubes.

After 12 wk, ~16 fish were randomly selected from each group, anaesthetized with tricaine methanesulfonate (MS-222), and individually weighed before the spinal cord was severed behind the head. Livers were dissected, weighed, frozen with liquid nitrogen, freeze-dried, and stored in a refrigerator until required for analysis. The livers were analyzed for glycogen content by the method of Murat and Serfaty (1974). Carcass samples were collected from each group, ground, freeze-dried, and stored in a refrigerator until required for proximate analysis as previously described.

Kidneys and livers were removed from 40 fish that were randomly sampled from each group, pooled into four groups

TABLE 1. Composition and analysis of the basal diet.[d]

Ingredient	Percentage
Capelin meal (CP[a] 68%)	56.3
Soybean meal (CP[a] 48%)	30.0
Corn starch	6.2
Vitamin mix[b]	2.5
Mineral mix[b]	1.2
Fish oil	3.8
Analysis[c]	
Crude protein	52.4±0.2
Crude lipid	14.0±0.1
Ash	8.2±0.1
Moisture	7.3±0.2
Crude fiber	1.9±0.2

[a]CP = crude protein.
[b]As given in diet 5 of Cho et al. 1974.
[c]Mean of three samples ± SD expressed on a dry matter basis.
[d]Alpha floc replaced basal diet as a whole so as not to alter nutrient balance.

TABLE 2. Growth characteristics of rainbow trout reared on feeding schedule A (10 and 20% fiber groups adjusted to ad libitum feeding level of 0% fiber group) and feeding schedule B (0 and 10% fiber groups adjusted to the ad libitum feeding level of the 20% fiber group) after 12 wk.

	Supplemental alpha-floc (%)					
	Feeding schedule A			Feeding schedule B		
	0	10	20	0	10	20
Weight gain (kg/100 fish ± SD)	4.6±0.5[c]	4.3±0.4[c,d]	3.9±0.5[d]	4.4±0.4[c]	4.2±0.4[c,d]	4.0±0.5[d]
Feed intake (kg/100 fish)	5.0	5.4	5.6	4.6	5.2	5.7
Allotted feed intake[a]	—	5.5	6.0	4.6	5.2	—
Feed:gain	1.2	1.3	1.5	1.1	1.2	1.5
Mortalities[b]	0.5	0.9	0.4	1.0	0.9	0

[a]Ten and 20% groups of schedule A calculated as 110 and 120% of feed intake of 0% group; 0 and 10% groups of schedule B calculated as 80 and 90% of feed intake of 20% group.
[b]Number of mortalities per 10 000 fish-days.
[c,d]Values in horizontal rows with same superscript are not significantly different ($P < 0.05$).

of ~10 fish per sample, and freeze-dried. The kidney, liver, and carcass content of copper, iron, and zinc was determined by atomic absorption spectrophotometry.

Gastric emptying time — The gastric emptying time was determined by the method of Hilton et al. (1981). After 12 wk on the test diets, fish of feeding schedule A were fed ad libitum, and then 30, 60, 180, and 360 min after feeding, four to six fish were randomly sampled from each group. The fish were anaesthetized with MS-222, weighed, killed, and the stomachs dissected from surrounding tissues and weighed. The feed-ingesta contents from each stomach were removed and the moisture content of the ingesta determined by the method of Horwitz et al. (1970). The empty stomach was then reweighed and the dry matter ingesta:fish weight, and dry matter ingesta:empty stomach ratios were determined.

Diet dry matter digestibility — Following the 12-wk test period, trout of feeding schedule A were fed the same test diets containing 1% chromic oxide (Fisher Chemical Co., Toronto, Ont., Canada) for 1 wk. All diets were fed to satiety during this period. About 40 fish from each group were then randomly sampled, killed, and their gastrointestinal tracts removed. Fecal samples were then obtained from the rectum and pooled to make up four fecal samples per group of ~10 fish-feces per sample. The samples were frozen at −20°C, freeze-dried, and stored for analysis.

Samples of test diets and freeze-dried feces were analyzed for chromium concentration by atomic absorption spectrophotometry (Arthur 1970) and moisture content. The apparent dry matter digestibility coefficient (DC) was calculated using the following formula:

$$DC = 100 - \left(100 \times \frac{\%Cr_2O_3 \text{ feed (dry matter)}}{\%Cr_2O_3 \text{ feces (dry matter)}}\right).$$

Statistical analysis — The results were analyzed by linear regression or analyses of variance using a split-plot design, and, where applicable, differences determined at the 5% level using Tukey's procedure (Steel and Torrie 1980).

Results — There was a significant linear regression of dietary fiber level on the weight gain and feed efficiency of trout in both feeding schedules (Table 2). There was no significant difference in the weight gain or feed:gain ratio of trout reared on the same dietary fiber level in feeding schedule A or B; however, there was a significant difference in the weight gain of trout reared on 0 as compared to 20% alpha-floc. Trout reared on diets of 10 and 20% alpha-floc in feeding schedule A were unable to eat sufficient feed to equal the nutrient levels consumed by the 0 alpha-floc group, whereas all fish in schedule B completely consumed their allotted feed. No significant difference was detected in the number of mortalities in the trout on the different dietary treatments.

No significant differences were detected in the hemoglobin, hematocrit, plasma glucose, or plasma protein levels of rainbow trout reared on the different dietary treatments for 12 wk. Liver glycogen, liver:body weight ratios, and proximate analysis of the freeze-dried carcasses (i.e. ash, crude protein, crude lipid, and dry matter content) were not significantly different in the trout fed the various dietary treatments for 12 wk. Similarly, no significant differences were detected in the kidney, liver, and carcass copper, iron, or zinc content of the trout on the different dietary treatments.

TABLE 3. Comparison of the dry matter digestion coefficient[a] (DC), estimated DC,[b] gastric emptying time,[c] and stomach:body weight ratio[d] of trout on feeding schedule A (fed ad libitum) after 12 wk on the test diets.

	(Supplemental alpha-floc level) (%)		
	0	10	20
DC	70.9±3.9	66.0±4.5	59.0±3.3
Estimated DC	—	63.8	57.6
Gastric emptying time (min)	782	379	412
Stomach:body weight ratio	1.4[e]	1.8[f]	1.9[f]

[a]Results are the mean of three samples ± SD.
[b]Assuming alpha-floc totally indigestible.
[c]Time for stomach to half empty, based on dry matter content of ingesta.
[d](Empty stomach weight ÷ body weight) × 100, results based upon the mean of 20 fish.
[e,f]Values in horizontal rows with same superscript are not significantly different ($P < 0.05$).

There was a decrease in gastric emptying time (Table 3), and a significant increase ($P < 0.05$) in the stomach size of trout reared on the high-fiber diets.

The dry matter digestibility of the diets was significantly decreased as the dietary fiber level increased (Table 3), and there was a significant linear regression of dietary fiber level on the digestion coefficient of the different dietary treatments. The digestion coefficients (DC) of the alpha-floc diets were somewhat higher than the expected or calculated values based on the assumption that the alpha-floc was totally indigestible.

Discussion — In this study 10 and 20% dietary fiber in the form of alpha-floc significantly ($P < 0.05$) reduced the growth rate of rainbow trout. There was essentially no difference in the weight gain, feed intake, and feed efficiency of trout fed the same dietary fiber level with feeding schedule A or B (Table 2) in which the feed intake of the trout was adjusted to that of trout reared on either the high-fiber or low-fiber diets. The trout appeared to adapt to increased dietary fiber and nutrient dilution by increasing feed consumption, but were unable to compensate completely for the high-fiber levels in feeding schedule A (Table 2). Lee and Putnam (1973) noted a similar response in trout fed diets with varying protein:energy ratios adjusted with cellulose, and the data from the present study support their conclusion that trout attempt to eat to satisfy their energy requirements. The heavier stomachs of trout reared on the high-fiber diets (Table 3) may indicate that the trout morphologically adjusted to the high-fiber diet by increasing either the stomach volume or distensibility so as to accommodate to the increased bulk of such diets. However, despite this possible morphological adaptation and increased feed consumption of trout on the high-fiber diets, the trout were unable to adapt completely to such diets. Regression analysis indicated that increased dietary fiber significantly ($P < 0.05$) reduced weight gain in rainbow trout. Trout reared on the 10 and 20% alpha-floc diets in feeding schedule A were unable to consume sufficient feed to obtain the same nutrient intake levels as trout reared on the no alpha-floc diet. This indicates that the growth depression of trout reared on the alpha-floc diets was due in part to a reduction in nutrient intake.

In contrast to feeding schedule A, trout reared on feeding schedule B consumed the same nutrient levels on all three diets, yet there was still a significant growth depression as the alpha-floc level increased (Table 2). This indicates that alpha-floc per se caused some of the growth depression.

Gastric emptying time was much faster in trout on the high-fiber diets than with the control although there was no apparent difference between the 10 and 20% fiber groups (Table 3). Grove et al. (1978) noted a similar response in trout fed diets diluted with kaolin. Adron et al. (1973) suggested that feeding frequency is related to gastric emptying in fish. Therefore, it is possible that a rapid gastric evacuation is a physiological adjustment of the trout designed to permit increased consumption of low energy diets.

Rainbow trout appear to have the ability to adapt morphologically and physiologically to increased dietary fiber; however, the limit of this adaptation is probably less than 10% dietary fiber, and fiber levels for trout diets should therefore be less than 10% of the diet. Although the digestibilities of the alpha-floc diets were not reduced as much as expected based on the assumption that alpha-floc was completely indigestible, considering the standard deviations associated with the determined digestion coefficients, it cannot be stated that any of the cellulose was being digested. It is possible that dilution of the diet with cellulose increased the digestibility of other nutrients as suggested by Buhler and Halver (1961).

Recent research has indicated that dietary fiber may affect the digestion and absorption of carbohydrates (Jenkins et al. 1976; Miranda and Horwitz 1978) and the uptake of minerals in terrestrial mammals (Harmouth-Hoene and Schelenz 1980; Renan and van Rensburg 1980). Plasma glucose and protein levels as well as liver glycogen content and liver:body weight ratios of the trout were not affected by the different dietary fiber levels in this study. The total amount of starch in the test diets was ~15%, of which only about 2 or 3% would be expected to be digested by trout (National Research Council 1981). Considering the low level of digestible carbohydrate in the test diets, it is not surprising that no effect of dietary fiber on carbohydrate digestion was detected in this study. It is well known that cellulose is less physiologically active than other types of fiber such as lignin and pectin in altering the uptake of dietary minerals (Harmouth-Hoene and Schelenz 1980; Renan and van Rensburg 1980). This may explain why no differences were detected in the other blood characteristics or the mineral content of the kidney, liver and carcasses of trout reared on the different levels of dietary fiber.

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ADRON, J. W., A. BLAIR, C. B. COWEY, AND A. M. SHANKS. 1976. Effect of dietary energy level and dietary energy source on growth, feed conversion and body composition of turbot (*Scophthaimus maximus* L.). Aquaculture 7: 125–132.

ARTHUR, D. 1970. The determination of chromium in animal feed and excreta by atomic absorption spectrophotometry. Can. J. Spectrosc. 15: 1–4.

BLIGH, E. G., AND W. G. DYER. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911–917.

BUHLER, D. R., AND J. E. HALVER. 1961. Nutrition of salmonid fishes. IX. Carbohydrate requirements of chinook salmon. J. Nutr. 74: 307–318.

CHO, C. Y., H. S. BAYLEY, AND S. J. SLINGER. 1974. Partial replacement of herring meal with soybean meal and other changes in a diet for rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 31: 1523–1528.

DUPREE, H. K., AND K. E. SNEED. 1966. Responses of channel catfish to different levels of major nutrients in purified diets. U.S. Bur. Sport Fish. Wildl. Tech. Pap. 9: 21 p.

GROVE, J. J., L. G. LOIZIDES, AND J. NOTT. 1978. Satiation amounts, frequency of feeding and gastric emptying in *Salmo gairdneri*. J. Fish. Biol. 12: 507–516.

HARMOUTH-HOENE, A. E., AND R. SCHELENZ. 1980. Effect of dietary fiber on mineral absorption in growing rats. J. Nutr. 110: 1774–1784.

HILTON, J. W., C. Y. CHO, AND S. J. SLINGER. 1981. Effect of extrusion processing and steam pelleting diets on pellet durability, pellet water absorption and the physiological response of rainbow trout (*Salmo gairdneri*). Aquaculture 25: 185–194.

HORWITZ, W., P. CHICHILO, AND H. REYNOLDS. [ed.] 1970. AOAC methods, official method of analysis of the official analytical chemists. 11th ed. Association of Official Analytical Chemists, Washington, DC. 1015 p.

JENKINS, D. J. A., D. V. GOFF, A. R. LEEDS, K. G. M. M. ALBERTI, T. M. S. WOLEVEC, M. A. GASSULL, AND T. D. R. HOCKADAY. 1976. Unabsorbable carbohydrates and diabetes: decreased postprandial hyperglycemia. Lancet 11: 172–174.

LEE, D. J., AND G. B. PUTNAM. 1973. The response of rainbow trout to varying protein/energy ratios in a test diet. J. Nutr. 103: 916–922.

LEARY, D. F., AND R. T. LOVELL. 1975. Value of fiber in production-type diets for channel catfish. Trans. Am. Fish. Soc. 104: 328–332.

LOWRY, O. H., N. J. ROSEBROUGH, A. L. FARR, AND R. J. RANDALL. 1951. Protein measurement with the Folin phenol reagent. J. Biol. Chem. 193: 265–275.

MIRANDA, P. M., AND D. L. HORWITZ. 1978. High-fiber diets and the treatment of diabetes mellitus. Ann. Int. Med. 88: 482–486.

MURAT, J. C., AND A. SERFATY. 1974. Simple enzymatic determination of polysaccharide (glycogen) content of animal tissues. Clin. Chem. 20: 1576–1577.

NATIONAL RESEARCH COUNCIL. 1977. Nutrient requirements of warmwater fishes. National Academy of Sciences, Washington, DC. 78 p.

NATIONAL RESEARCH COUNCIL. 1981. Nutrient requirements of coldwater fishes. No. 16. Nutrient requirements of domestic animals. National Academy Press, Washington, DC. 63 p.

RENAN, M. J., AND S. J. VAN RENSBURG. 1980. The influence of high-bran diets on trace element retention in primates. Phys. Med. Biol. 25: 433–444.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics. McGraw Hill, New York, NY. 661 p.

Mercury Speciation in Water

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RAMAMOORTHY, S., T. C. CHENG, AND D. J. KUSHNER. 1983. Mercury speciation in water. Can. J. Fish. Aquat. Sci. 40: 85–89.

Speciation of mercury in water and in the air above the water was studied. The effects of hydrogen peroxide, bacterial growth medium, and both living and dead bacteria (*Escherichia coli* and *Pseudomonas aeruginosa*) were tested. Both living and dead bacteria transport metallic mercury from water into air. The amount of total Hg produced in the head space was similar in living or dead bacterial and hydrogen peroxide systems, $\simeq$7 μg/L. Hydrogen peroxide stabilized Hg^{2+} in the system. Partition coefficients were calculated from the corrected concentrations in the head space using literature solubility values for air/water phases. It is possible that Hg^0 could be produced biologically or/and abiologically in a microenvironment within suspended particulate matter under favorable conditions. Further movement into air or subsequent transformation would depend on the physicochemical properties of the bulk water.

Key words: mercury speciation, water, bacterial growth medium, living and dead bacteria

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On a étudié la transformation du mercure dans l'eau et dans l'air au-dessus de l'eau. On a analysé les effets du peroxyde d'hydrogène, le milieu de culture des bactéries, de même que les bactéries mortes et vivantes (*Escherichia coli* et *Pseudomonas aeruginosa*). Les bactéries mortes et vivantes transportent toutes deux le mercure inorganique de l'eau dans l'air. La quantité totale de Hg produite au-dessus de l'eau était identique dans les systèmes utilisant des bactéries mortes ou vivantes et du peroxyde d'hydrogène, c'est-à-dire $\simeq$7 μg/L. Le peroxyde d'hydrogène a stabilisé le mercure sous forme de Hg^{2+} dans le système. Les coefficients de séparation ont été calculés à partir des concentrations corrigées au-dessus de l'eau en se servant des valeurs de solubilité connues pour les phases air/eau. Il est possible que le Hg^0 puisse être produit ou non par des organismes dans un milieu microscopique à l'intérieur de particules en suspension lorsque les conditions sont favorables. Un déplacement

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ultérieur dans l'air ou une transformation subséquente dépendraient des propriétés physico-chimiques de la masse d'eau.

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MERCURY enters the environment through a number of natural and industrial processes and is found in several different chemical forms. Bacteria are involved either in the alkylation of Hg^{2+} or its reduction to Hg^0; a number of mercury-resistant bacteria have been shown to convert Hg^{2+} and other Hg compounds into the less toxic form, Hg^0 (Nelson et al. 1973; Summers and Lewis 1973). Hg^0 is also released into the environment by many industrial and natural processes (D'Itri 1972). However, the fate of Hg^0 in natural waters has been little studied. The only relevant information consists of E_h-pH diagrams in deionized water (Hem 1970). The literature is lacking in information regarding mercury speciation in aqueous systems containing different substrates. It seems essential to have further information on this subject, especially because alkylation of mercury to its most toxic forms depends on the presence of free Hg^{2+} ions (Bisogni and Lawrence 1975) and possibly Hg^0 under slower anaerobic alkylation (D'Itri 1972). In the present study, we have investigated the transformation of Hg^0 into other forms in water as well as the release of Hg^0 and other forms of mercury into the air above the water. The effects of H_2O_2, bacterial growth medium which contains a number of Hg^{2+}-binding compounds (Ramamoorthy and Kushner 1975), and of both living and dead bacteria (*Escherichia coli* and *Pseudomonas aeruginosa*) were also tested.

Materials and methods — Double-distilled metallic mercury (Engelhard, Canada) was used in this study. All analyses of elemental mercury, and its oxidized and alkylated forms, were carried out by flameless atomic absorption spectroscopic methods (Ottawa River Project, Final Report 1977; Environment Canada 1977). For the analysis of elemental mercury species in the water column, samples were purged with nitrogen gas without the addition of the reducing agents, stannous chloride or stannous chloride and cadmium. Measurements of pH or oxidation–reduction potentials (ORP) were made with the Orion ionalyzer model 801 using the glass electrode or the combination redox-electrode model 96-78 (Orion Research Inc.), respectively. The experiments were conducted at room temperature, 20 ± 1°C.

The experimental chamber was a 6-L Pyrex conical flask with two side arms (Fig. 1). The upper shorter side arm (diameter 15 mm) was sealed with a silicone rubber septum (Hamilton septum, 760-16) enclosed in a screw cap. The septum was coated with a layer of polymeric silicone fluid (Dri-Film Sc-87, Chromatographic Specialities) which is highly inert chemically. The lower longer side arm was closed by a ground glass stopper.

Sixty-four microlitres (i.e. 870 mg) of metallic mercury was introduced into 5 L of deionized water in the reaction vessel. This amount of metallic mercury exceeds the solubility of elemental mercury in water, reported as 25–30 μg/L (Krenkel 1974), and was used to maintain mass flow following species transformation. The water was continuously stirred magnetically, except during sample withdrawal. Stirring was stopped 15 min prior to sampling in order that the metallic mercury would settle to the bottom of the flask. This procedure should avoid any possibility of trapping metallic mercury during sampling.

Aliquots of the water column were withdrawn at intervals of 0, 3, 6, 9, 12, 24, 48, 72, 96, 120, and 240 h through the longer side arm and then analyzed for mercury species. Simultaneously with water sampling, 5 mL of the air in the head space over the water column was withdrawn by a disposable syringe through the septum on the shorter arm. Rather than analyzing the head space air directly, air was emptied into 2 mL of water and vigorously shaken to maximize partition and match the analytical conditions of the aqueous phase. It was then analyzed for Hg^0 and Hg^{2+} species. It is quite possible that some aerial oxidation of Hg^0 took place during or after equilibration with the receiving water introducing ionized forms of Hg in the head space. Hence only total mercury is reported in the head space, although some ionized Hg was found in the analyses. Thus, partitioning of metallic mercury was comparable for both head space and aqueous phase in the analytical end of the experiment. Partition coefficients calculated from the corrected concentrations in the head space using literature solubility values for air/water phases (Moser and Voight 1957) are 0.39–0.40 in good agreement with 0.40 reported by Koirtyohann and Khalil (1976).

Mercury species were analyzed after the following chemicals and bacteria were added to metallic mercury in the reaction vessel: (1) deionized distilled water, (2) deionized distilled water with 0.3% H_2O_2, (3) sterilized growth medium of Foot and Taylor (FT) (Foot and Taylor 1949), (4) FT medium containing growing *E. coli* B/r or *P. aeruginosa*, NRCC 5005, (5) deionized water containing thermally killed *E. coli* or *P. aeruginosa*. The bacteria studied here are commonly present in natural waters.

The results are presented in Fig. 2–4, giving mercury speciation as total Hg for head space and Hg^0 and Hg^{2+} species for the aqueous phase as a function of time. No organic forms of mercury were detected using a differential reduction method (Ottawa River Project, Final Report 1977; Environment Canada 1977) in the systems studied in this work. As biological methylation is <0.1% of total mercury, methylmercury formed, if any, at concentrations of mercury (<30 μg/L) in bacterial systems studied here would be well below detection by atomic absorption method.

The bacteria were grown in peptone–yeast extract medium (PYEB) (2% peptone and 0.15% yeast extract, pH 7) to initial stationary phase and harvested. The cells were washed with deionized water at least five times, then weighed. About 2 g wet weight of cells were killed by boiling in deionized water for 30 min, then added to the experimental chamber containing 5 L of deionized water.

For the study of transformation of metallic mercury by

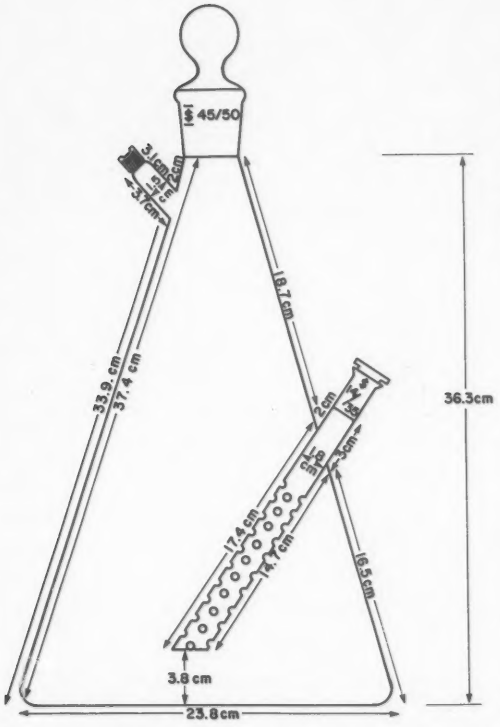

FIG. 1. Experimental chamber designed for the study of transformation of metallic mercury.

growing bacteria, the preculture was grown in FT medium to the end of the logarithmic phase, then 25 mL of the preculture was transferred to 5 L of sterilized FT medium containing metallic mercury in the experimental chamber. Growth of bacteria in this system was followed by optical density readings and viable cell counts.

Results and discussion — In deionized water, after ~24 h, the amount of Hg^0 in the aqueous phase increases with time, slowly reaching 33 μg/L at 240 h. This amount corresponds to the solubility of Hg^0 in water (Krenkel 1974). The concentration of total Hg in the head space (about 1/5 of the water column volume) reaches 5 μg/L. This is three times the concentration of Hg^{2+} species in the deionized water which in a closed system produces more Hg^0 than Hg^{2+} in the aqueous phase.

If 0.3% H_2O_2 is added to deionized water, the speciation of mercury is quite different from that in deionized water alone (Fig. 2), with the level of Hg^{2+} in the aqueous phase after 96 h increasing by about 8000 times. This is due to the higher oxidizing capacity of H_2O_2 than deionized water. The total [Hg] is about 2.2 times higher in the head space (Fig. 2) in H_2O_2 than in deionized water, and the speciation seems to reach a "steady state" in 120 h.

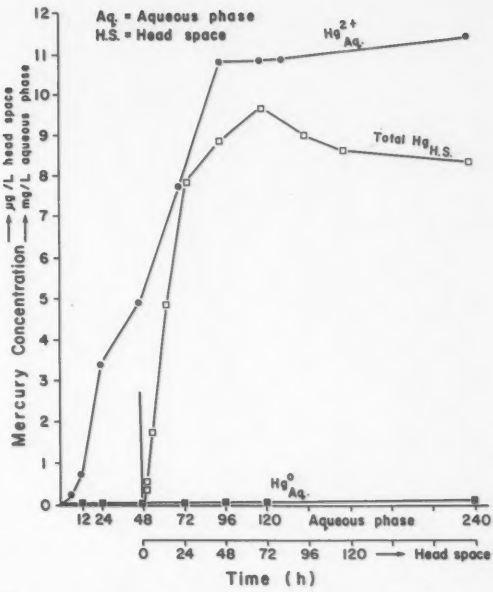
Aq. = Aqueous phase
H.S. = Head space
$Hg^{2+}_{Aq.}$
Total $Hg_{H.S.}$
$Hg^0_{Aq.}$
Mercury Concentration → μg/L head space → mg/L aqueous phase
0 1 2 3 4 5 6 7 8 9 10 11 12
12 24 48 72 96 120 Aqueous phase 240
0 24 48 72 96 120 → Head space
Time (h)

FIG. 2. Speciation of mercury in deionized water with 0.3% H_2O_2.

Figure 3 presents the results of metallic mercury speciation in FT medium with and without growing bacteria. [Hg^0] in the aqueous phase in FT medium is 31 μg/L (maximum solubility) and 4 μg/L in the head space, reaching a "steady state" in ~96 h. However, the [Hg^{2+}] species in the aqueous phase reached 9 μg/L at "equilibrium state" at 96 h, which is higher than that found in the deionized water system. This may be because inorganic and organic components of the FT medium can form complexes with the Hg^{2+} ion and stabilize it in the aqueous phase.

In the presence of living *E. coli* or *P. aeruginosa*, the total mercury concentration in the head space was about the same for both bacteria and for sterilized FT medium for the first 24 h (Fig. 3). However, the biological action on transformation of metallic mercury was obvious at 48 h, and at the end of 240 h there was about 5 μg/L of total Hg in the head space in the FT medium–*E. coli* system and 8 μg/L in the FT medium–*P. aeruginosa* system. The level of Hg^{2+} in the aqueous phase was slightly higher in the presence of living bacteria, especially *E. coli*, than in the FT medium alone, by a factor of two which is environmentally significant. However, the level of Hg^0 in the aqueous phase was about the same as in the FT medium (Fig. 3). Viable cell counts showed that the bacteria grew well in the medium. The number of cells were the same both in control and in the mercury-added FT medium for both bacteria (results not shown).

The results of experiments with thermally killed bacteria are shown in Fig. 4. The amount of total Hg in the head space was about the same in both systems up to 72 h; then it was higher in the flask with *P. aeruginosa*. At the end of 240 h, about 7 μg/L of total mercury in the head space was obtained

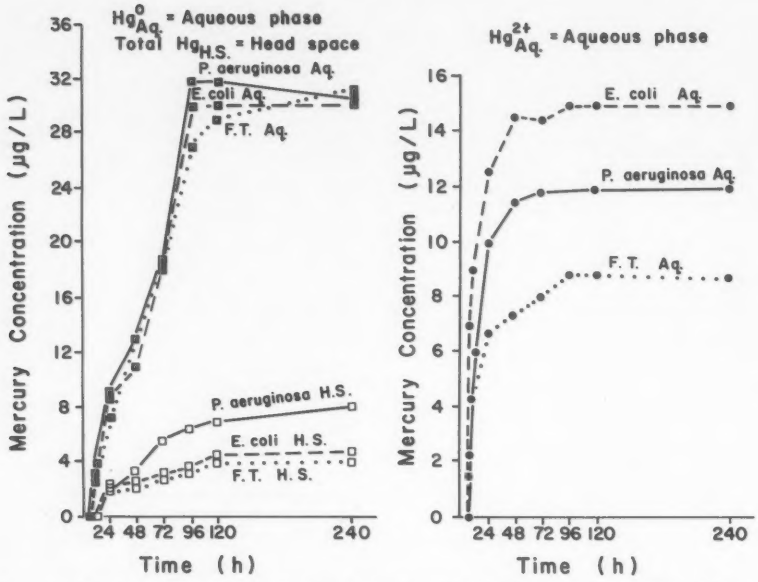

FIG. 3. Speciation of mercury in Foot and Taylor (FT) medium with and without growing bacteria, *Pseudomonas aeruginosa* or *Escherichia coli*.

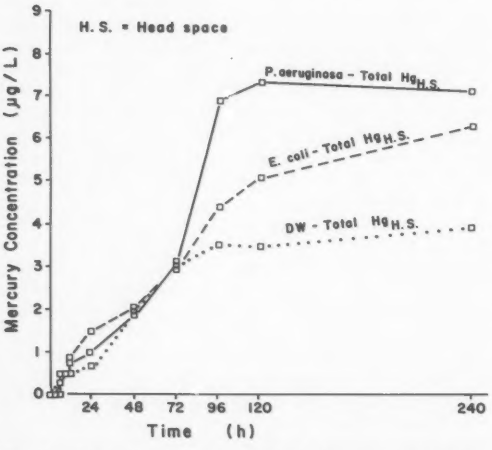

FIG. 4. Speciation of mercury in deionized water containing thermally killed bacteria, *Pseudomonas aeruginosa* or *Escherichia coli*.

for both bacterial systems. The amount in the aqueous phase could be calculated using the partition coefficient values.

At "equilibrium state" (about 120–240 h), the amount of total Hg in the head space is about the same for both the dead or living bacteria (Fig. 3 and 4). However, total weight (2 g wet weight) of dead cells was less than that of living cells in stationary phase (about 7.5 g wet weight for *E. coli* and 12.5 g wet weight for *P. aeruginosa*) at 240 h. It seems that dead cells are more efficient than living cells in accelerating the dissolution of metallic mercury in water and then volatilizing it into the head space. This suggests that thermal killing of bacteria might expose the internal structures and release the intracellular Hg-binding components.

From the above studies, it is clear that the bacteria chosen, either living or thermally killed, possess the ability to transport metallic mercury from water into air. The amount of total Hg produced in the head space was almost the same in living or dead bacterial and hydrogen peroxide systems and was around 7 μg/L. The redox potential of the systems was 425 ± 24 mV with reference to the standard calomel electrode, and generally the redox potential dropped during the experiment. The pH of the systems did not change during the experimental period; 6·8 for the deionized water and H_2O_2 system and 7·1 for the growth medium and the bacterial systems. Hydrogen peroxide stabilized Hg^{2+} in the system. The possibility of Hg^0 being produced in natural waters depends on the types of chemical and biological moities present, which might provide reducing conditions. The redox potential might vary from the bottom of the water (anaerobic) to the upper level of the water (aerobic) in a flowing river. Hence in this study, to simulate the natural condition, the variables such as pH and redox potentials were not fixed. It is possible that Hg^0 could be produced in a microenvironment through biological or abiological pathways and further movements to air from the water or subsequent transformation of this Hg^0 will depend on the physicochemical conditions of the bulk water.

BISOGNI, J. J., AND A. W. LAWRENCE. 1975. Kinetics of mercury methylation in aerobic and anaerobic environments. J. Water Pollut. Control Fed. 47: 135–152.

D'ITRI, F. M. 1972. The environmental mercury problem. Chemical Rubber Co. Press, Cleveland, OH. 124 p.

ENVIRONMENT CANADA. 1977. Mercury: methods for sampling, preservation and analysis: A Report to the Environmental Contaminants Program Steering Committee of Fisheries and Environment Canada, Ottawa.

FOOT, C. H., AND C. B. TAYLOR. 1949. The influence of the composition of the medium on the growth of bacteria from water. Proc. Soc. Appl. Bacteriol. 1: 11–13.

HEM, J. D. 1970. Chemical behavior of mercury in aqueous media. *In* Mercury in the environment, Geol. Surv. Pap. 713, U.S. Government Printing Office, Washington, DC.

KOIRTYOHANN, S. R., AND M. KHALIL. 1976. Variables in the determination of mercury by cold vapor atomic absorption. Anal. Chem. 48: 136–139.

KRENKEL, P. A. 1974. Mercury: environmental considerations, Part II. CRC Crit. Rev. Environ. Control 4: 251–339.

MOSER, H. C., AND A. F. VOIGHT. 1957. Dismutation of mercurous dimer in dilute solutions. J. Am. Chem. Soc. 79: 1837–1839.

NELSON, J. D., W. BLAIR, F. E. BRINCKMAN, R. R. COLWELL, AND W. P. IVERSON. 1973. Bio-degradation of phenylmercuric acetate by mercury-resistant bacteria. Appl. Microbiol. 26: 321–326.

OTTAWA RIVER PROJECT, FINAL REPORT. 1977. Distribution and transport of pollutants in flowing water ecosystems. Natl. Res. Counc. Can. Ottawa, Canada. 1165 p.

RAMAMOORTHY, S., AND D. J. KUSHNER. 1975. Binding of mercuric and other heavy metal ions by microbial growth media. Microb. Ecol. 2: 162–176.

SUMMERS, A. O., AND E. LEWIS. 1973. Volatilization of mercuric chloride by mercury-resistant plasmid-bearing strains of *E. coli*, *Staphylococcus aureus* and *Pseudomonas aeruginosa*. J. Bacteriol. 113: 1070–1072.

Use of NaCl as a Reference Toxicant for Goldfish, *Carassius auratus*

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THREADER, R. W., AND A. H. HOUSTON. 1983. Use of NaCl as a reference toxicant for goldfish, *Carassius auratus*. Can. J. Fish. Aquat. Sci. 40: 89–92.

The 240-h NaCl LC50 for goldfish, *Carassius auratus*, was estimated as 201.1 (SE 6.7) mmol · L^{-1}, a concentration well in excess of one recently published value, but consistent with earlier observations on the tolerance of this species for hypersaline conditions. Evidence for operation of several lethal effects that vary in intensity with time, the absence of a well-defined relationship between dose and mortality within an intermediate range of lethal NaCl concentrations, and the strong likelihood of size-related variation in individual sensitivity to NaCl suggest that NaCl is an inappropriate reference toxicant for use in static bioassays involving this species.

Key words: NaCl, goldfish, toxicity

THREADER, R. W., AND A. H. HOUSTON. 1983. Use of NaCl as a reference toxicant for goldfish, *Carassius auratus*. Can. J. Fish. Aquat. Sci. 40: 89–92.

Après 240 h d'exposition, la CL 50 de NaCl du poisson doré, *Carassius auratus*, s'élève à 201,1 (SE 6,7) mmol L^{-1}, concentration nettement supérieure à une autre récemment publiée, mais conforme aux observations antérieures sur la tolérance de cette espèce envers des conditions hypersalines. Les faits suivants portent à croire que le NaCl n'est pas une substance toxique appropriée comme base de référence pour l'expérimentation biologique statique portant sur cette espèce : le fait que plusieurs effets létaux agissent et leur intensité varie dans le temps, l'absence d'une relation bien définie entre la dose et la mortalité aux concentrations létales moyennes de NaCl et la forte probabilité d'une relation entre la taille de l'individu et la sensibilité au NaCl.

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STANDARDIZATION of bioassay procedures has been recommended as a means of facilitating comparison of toxicity data obtained in different laboratories (e.g. Marking 1966; Sprague 1973; Davis and Hoos 1975). Use of selected test species has been proposed, as has the routine testing of assay populations against reference toxicants and the expression of test substance toxicity in relation to that of one or more reference materials.

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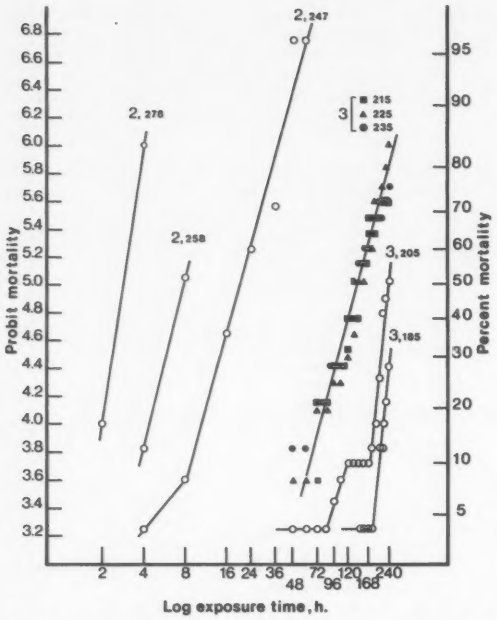

FIG. 1. Accumulative mortality in goldfish exposed in Series 2 and Series 3 trials to various NaCl concentrations (mmol·L^{-1}).

Following studies involving several possible reference toxicants and a number of commonly used test species, Adelman and Smith (1976) and Adelman et al. (1976a, b) concluded that NaCl was superior in many respects to alternative standards and particularly useful in static assays. The reported 96-h LC50 (~125 mmol·L^{-1}) for goldfish (*Carassius auratus*), one of the species considered, was, however, within normal limits for plasma sodium and chloride concentrations (Prosser et al. 1970; Murphy and Houston 1974; McCarty and Houston 1976). Death of stenohaline fishes in hypersaline media involves osmoregulatory failure, and this would not be expected under essentially isotonic conditions. Moreover, goldfish reportedly tolerate substantially higher NaCl concentrations (e.g. 200–240 mmol·L^{-1}) for extended periods (Black 1951; Nishihara 1953). The present study was undertaken primarily to examine this anomaly.

Materials and methods — Goldfish (0.38–4.02 g) were obtained from a commercial supplier and acclimated to the test temperature used (23.5°C) for at least 2 wk prior to trials. A 12-h light:12-h darkness photoperiod regime was maintained throughout holding and testing. Animals were fed twice daily ad libitum during this period. No mortality was encountered prior to testing, and the animals appeared healthy and active.

Static bioassays were conducted in 100-L Fiberglass aquaria which were thoroughly washed and rinsed in deionized distilled water before each trial. Well-aerated, dechlorinated, and aged St. Catharines city water of moderate total hardness and alkalinity was used. All tanks were provided with laterally positioned submerged air bars for aeration and mixing. Translucent plastic hoods reduced evaporative water loss and visual disturbance of fish.

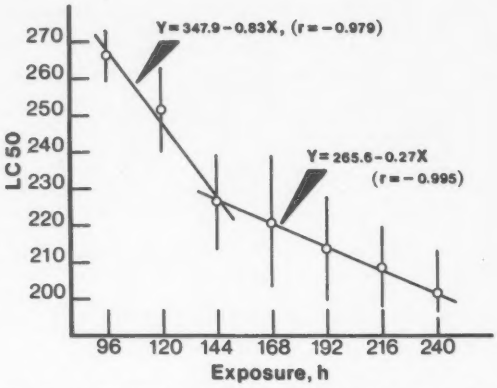

FIG. 2. NaCl LC50 (mmol·L^{-1}) in relation to duration of exposure. Vertical line: SE of estimated LC50.

Feeding was terminated 24 h before transfer to test tanks, and fish were not fed during trials. Following a 2-d period for recovery from transfer, we siphoned residual fecal and other materials from the tanks. Test concentrations were then established by addition of appropriate amounts of analytical grade NaCl (Fisher Analar) dissolved in small volumes of distilled water. Water level indicators sensitive to volume changes of ~20 mL allowed for early detection of and correction to evaporative water losses. Water samples were withdrawn by fixed siphons at 0, 24, 48, 96, and 240 h and sodium and chloride concentrations determined using a Unicam SP-90 AAS and Buchler–Cotlove chloridometer. During trials of up to 21 d duration, mean standard error for NaCl variation was 0.53 mmol·L^{-1} (range: 0.05–1.28 mmol·L^{-1}). Total hardness and alkalinity, pH, and dissolved oxygen were measured daily.

We carried out three series of tests. The first (Series 1) was essentially a repetition of earlier studies and involved exposures to 90, 100, 110, 120, 125, 130, and 140 mmol·L^{-1} NaCl. As these led to low and inconsistent mortalities we conducted a second set of tests (Series 2) using a broader range of concentrations (188, 215, 247, 258, and 306 mmol·L^{-1}). A final series (Series 3) involving 185, 205, 215, 225, and 235 mmol·L^{-1} NaCl was then used to refine the LC50 value generated in Series 2. Trials were replicated to provide totals of 25 (Series 1) or 50 fish (Series 2, 3) per test concentration at densities below 0.25 g fish·L^{-1}. Each tank was examined at 1, 2, 4, 8, 16, and 24 h and thereafter at 12-h intervals. We considered fish to be dead when they were immobile, without respiratory activity, and unresponsive to probing. LC50 estimates were carried out as described by Sprague (1973).

Results and discussion — Initial water-quality values

(mean ± SD) were total hardness: as $CaCO_3$, 148.8 ± 1.8 mg·L^{-1} (mean ± SD), total alkalinity: as $CaCO_3$, 100.0 ± 1.6 mg·L^{-1}, dissolved oxygen: 7.2 ± 0.1 mg·L^{-1}, pH: 7.95 ± 0.02. Total hardness decreased slowly during the 10-d period of most trials, falling on average by 7.9 mg·L^{-1} with little variation between tanks. This was also true of alkalinity which decreased by 6.7 mg·L^{-1}. Oxygen regularly exceeded 75% saturation, and pH variations were well within limits regarded as acceptable for assays of this type (Sprague 1973).

No deaths occurred between 0 and 84 h in Series 1, and thereafter only irregularly. Despite extension of trials at the higher test concentrations to 21 d, accumulative mortality never exceeded 24%, and no consistent relationship between concentration and mortality was evident.

In Series 2 total mortality was observed from 1 to 8 h in 258, 278, and 306 mmol·L^{-1} test solutions, and after 60 h at 247 mmol·L^{-1}. Survival was much prolonged at lower concentrations; 240-h accumulative mortalities in 188 and 215 mmol·L^{-1} solutions being 64 and 92%, respectively. The estimated 240-h LC50 was ~200 mmol·L^{-1}.

Mortality data for the final series of trials (Series 3) are summarized in Fig. 1. The 240-h LC50 estimated from these data was 201.1 mmol·L^{-1} (SE ± 6.7 mmol·L^{-1}). Although substantially higher than that reported by Adelman and Smith (1976) and Adelman et al. (1976a, b), this value compares favorably with previously reported tolerances in goldfish (Black 1951; Nishihara 1953) and is, of course, well in excess of normal plasma concentrations.

Whereas the basis of the discrepancy between the present and previously reported estimates of NaCl toxicity to goldfish is not evident, several procedural differences existed between the two studies (I. R. Adelman, Department of Entomology, Fisheries and Wildlife, University of Minnesota, 1980, personal communication). Animals were fed throughout the earlier study. Consequently, their metabolic activity and thus oxygen demands were presumably higher than those of our present unfed fish. Under such conditions ventilation would be enhanced, with a consequent increase in toxicant presentation to the gills. Higher rates of NaCl uptake would then be expected. Ambient ammonia levels were elevated, and this may have adversely affected osmoregulatory ability. Three days prior to trials, test fish were shifted from relatively hard (~250 mg·L^{-1}, $CaCO_3$) to relatively soft (~60 mg·L^{-1}) water and may have been incompletely adapted to these conditions when tested. Possibly water–electrolyte metabolism, and consequently resistance to hypersaline conditions were impaired to some extent. It is difficult, however, to envisage effects so serious as to result in death under near-isotonic conditions.

A number of the observations made in this study suggest that NaCl is an inappropriate reference toxicant for use in bioassays involving goldfish. As is commonly the case estimates of LC50 decreased as exposure time increased. However, in this instance variations in LC50 with time appeared to follow a biphasic pattern. Using maximum coefficient of determination as a criterion, the relationship between LC50 and exposure time was less well fitted by continuous linear, power, and logarithmic functions than by two linear equations covering 0–144 and 144–240 h (Fig. 2). We suggest, therefore, that more than one principal cause of death operates, and that these vary in intensity with time.

A further complication was introduced by the sharp increase in accumulative mortality between 205 and 215 mmol·L^{-1}, the absence of concentration-dependent changes between 215 and 235 mmol·L^{-1}, and the secondary increases which ensued at higher concentrations (i.e. Series 2). The basis of this was not determined, but may reflect the nature of ionic regulation in freshwater teleosts. In freshwater, both sodium and chloride uptake are active processes. Accordingly, the gills are presumably characterized by a finite number of transport sites for each ion. If this is the case the observed dose–mortality plateau may reflect a range of concentrations within which transport sites are essentially saturated, but the lamellar epithelium is not excessively damaged. Given such circumstances, increases in toxicant concentration would not lead to increases in uptake, and mortality rates would presumably not vary with dosage. At higher concentrations, with more direct damage to respiratory surfaces, mortality might again be a function of concentration.

There are also grounds for anticipating weight-dependent variations in individual resistance to NaCl stress. Because sodium and chloride are primarily extracellular ions, their initial toxic effects are presumably exerted at the boundary between interstitial fluid and cells. A variety of these, ranging from osmotic dehydration to direct membrane interactions and their sequelae can be visualized. In any event, it is reasonable to assume that extracellular sodium and chloride levels must reach some critical threshold before significant abnormalities occur. This being the case, the gill area available for ion uptake becomes critical in relation to the extracellular volume to be raised to threshold concentration. Both are negative exponential functions of weight. Studies on induction of tricainemethane sulfonate anesthesia in goldfish — a convenient model of systems subject to such considerations — suggest that the ratio, weight-specific gill area:weight-specific extracellular volume, increases with weight (Houston et al. 1976). Thus, at equivalent concentrations smaller fish are affected less rapidly than are larger animals. Our study, which involved only a limited range of specimen weights, provided only tenuous evidence of weight-related differences in toxicant action. However, such effects have been noted in a number of other studies (e.g. Adelman et al. 1976c).

In summary, LC50 values for NaCl vary discontinuously with time, and may reflect time-dependent variations in cause of death. Within an intermediate range of test concentrations mortality is not a simple function of dosage. This has serious and obvious implications with respect to selection of reference toxicant concentrations and the validity of resulting LC50 estimates. There are reasonable grounds for anticipating that test organism size may influence apparent toxicity. These considerations mediate against the use of NaCl as a reference toxicant in bioassays involving goldfish.

ADELMAN, I. R., AND L. L. SMITH JR. 1976. Fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*) as standard fish in bioassays and their reaction to potential reference toxicants. J. Fish. Res. Board Can. 33: 209–214.

ADELMAN, I. R., L. L. SMITH JR., AND G. D. SIESENNAP. 1976a. Acute lethal effects of sodium chloride, pentachlorophenol, Guthion®, and hexavalent chromium to fathead minnows (*Pimephales promelas*) and goldfish (*Carassius auratus*). J. Fish. Res. Board Can. 33: 203–208.

1976b. Effect of size or age of goldfish and fathead minnows on use of pentachlorophenol as a reference toxicant. Water Res. 10: 685–687.

BLACK, V. S. 1951. Osmotic regulations in teleost fishes. Publ. Ont. Fish. Res. Lab. No. 71, Univ. Toronto Stud. Biol. Ser. 59: 53–89.

DAVIS, J. C., AND R. A. W. HOOS. 1975. Use of sodium pentachlorophenate and dehydroabietic acid as reference toxicants for salmonid bioassays. J. Fish. Res. Board. Can. 32: 411–416.

HOUSTON, A. H., J. T. CORLETT, AND R. J. WOODS. 1976. Specimen weight and MS 222. J. Fish. Res. Board Can. 33: 1402–1407.

MARKING, L. L. 1966. Evaluation of p,p'-DDT as a reference toxicant in bioassays. U.S. Bur. Sport Fish. Wildl. Resour. Publ. 14: 1–10.

MCCARTY, L. S., AND A. H. HOUSTON. 1976. Effects of exposure to sublethal levels of cadmium upon water–electrolyte status in the goldfish (*Carassius auratus*). J. Fish Biol. 9: 11–19.

MURPHY, P. G. F., AND A. H. HOUSTON. 1974. Environmental temperature and the body fluid system of freshwater teleost. V. Plasma electrolyte levels and branchial microsomal (Na^+/K^+) ATPase activity in thermally-acclimated goldfish (*Carassius auratus*). Comp. Biochem. Physiol. 47B: 563–570.

NISHIHARA, H. 1953. On the changes of chlorine content of goldfish in seawater. Sci. Rep. Saitama Univ. Ser. B, 1: 71–75.

PROSSER, C. L., W. MACKAY, AND K. KATO. 1970. Osmotic and ionic concentrations in some Alaskan fish and goldfish from different temperatures. Physiol. Zool. 43: 81–89.

SPRAGUE, J. B. 1973. The ABC's of pollutant bioassay using fish, p. 6–30. *In* J. Cairns Jr. and K. L. Dickson [ed.] Biological methods for the assessment of water quality. Am. Soc. Test. Mater. Spec. Tech. Publ. 528.

Total Dissolved Solids as a Predictor of Lake Biomass and Productivity

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PREPAS, E. E. 1983. Total dissolved solids as a predictor of lake biomass and productivity. Can. J. Fish. Aquat. Sci. 40: 92–95.

Total dissolved solids (TDS) and chlorophyll *a* were not related in 25 lakes which were all off the Precambrian Shield. Both on-shield and off-shield lakes were included in the previous reports which showed a significant relationship between TDS and productivity. When data from on-shield and off-shield lakes were analyzed separately, there was no significant positive relationship between TDS and lake biomass or productivity. It was also shown that mean depth ($\bar{z}$) was as good a predictor of fish production as the TDS:$\bar{z}$ ratio, the morphoedaphic index.

Key words: TDS, biomass, productivity, morphoedaphic index, chlorophyll *a*, lakes

PREPAS, E. E. 1983. Total dissolved solids as a predictor of lake biomass and productivity. Can. J. Fish. Aquat. Sci. 40: 92–95.

Il n'y a pas de relation entre les solides dissous totaux (SDT) et la chlorophylle *a* dans 25 lacs, tous hors du Bouclier précambrien. Dans les rapports antérieures, les lacs, tant du Bouclier qu'en dehors, avaient été inclus et avaient montré une relation significative entre les SDT et la productivité. Quand les données de ces deux types de lacs sont analysées séparément, cependant, on ne trouve aucune relation positive entre les SDT et la biomasse ou la productivité. Nous démontrons également que la profondeur moyenne ($\bar{z}$) est tout aussi utile que le rapport SDT:$\bar{z}$, l'indice morphoédaphique, pour prédire la production en poisson.

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TOTAL dissolved solids (TDS) was identified as an indicator of benthic, planktonic, and fish biomass, and fish production by Rawson (1951, 1960). Later the ratio of TDS to mean depth ($\bar{z}$), the morphoedaphic index (MEI), was developed to predict fish production (Ryder 1965). The criteria for use of the MEI for a group of lakes (i.e. where both TDS and $\bar{z}$ are important parameters) are that the lakes should be subject to a relatively homogeneous set of environmental conditions, with the exceptions that $\bar{z}$ and TDS should vary over a wide range (Ryder et al. 1974) or the lakes are part of a sizable region (Ryder 1982). The MEI has been widely used for lake management, although more recent investigations have shown that chlorophyll concentration (Oglesby 1977), benthic biomass (Matuszek 1978), and concentration of total phosphorus (Hanson and Leggett 1982) were better predictors of fish production than either TDS or the MEI.

Hanson and Leggett have suggested that TDS should be correlated with total phosphorus (TP) because phytoplankton

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TABLE 1. Relationships between total dissolved solids (TDS) and indices of productivity from reports which include lakes both on and off the Precambrian Shield. All correlations are log−log. Negative correlations are indicated by −, significant correlations by * ($P < 0.05$) or ** ($P < 0.01$).

		Lakes								
	Variables	All areas			On-shield			Off-shield		
Source	TDS vs.	n	r^2	P	n	r^2	P	n	r^2	P
Rawson 1961	fish production	12	0.50	0.01**	6	0.23	0.33	6	0.03	0.73
	fish catch	13	0.21	0.12	6	0.79⁻	0.02*	7	0.03⁻	0.98
	plankton biomass	13	0.23	0.10	6	0.43	0.16	7	0.03	0.73
	benthic biomass	13	0.59	0.00**	6	0.31	0.25	7	0.00	0.94
Ryder 1965	fish production	23	0.12	0.11	9	0.00⁻	0.90	14	0.24	0.08
Matuszek 1978	fish production	22	0.19	0.04*	10	0.15	0.27	12	0.03	0.58
	benthic biomass	11	0.43	0.03*	5	0.54	0.16	6	0.15	0.45
	plankton biomass	11	0.49	0.02*	5	0.39	0.26	6	0.20	0.37
Hanson and Leggett 1982[a]	fish production	40	0.14	0.02*	24	0.00⁻	0.76	16	0.11	0.20
	benthic biomass	26	0.54	0.00**	12	0.07	0.40	14	0.02	0.63

[a]Three lakes, Ijssel and Upper and Lower Constance, were excluded from the analysis because of uncertainty associated with the TDS-yield values. For Ijssel TDS was reported as chloride (Willemsen 1977) and ranged in other reports from 200 to 300 mg/L (J. M. Hanson personal communication). Hanson and Leggett used a mean value of 250 mg TDS/L, which made Ijssel an outlier, 30% higher than any other lake in the set. When Lake Constance underwent eutrophication, fish yield increased threefold whereas TDS remained constant (Hartmann and Nümann 1977). Hanson and Leggett used only posteutrophication yield data which were not unique with respect to TDS. When these three lakes are excluded there is no significant log−log relationship between TDS and total phosphorus ($n = 18$, $r^2 = 0.06$, $P = 0.31$).

biomass and production in lakes are dependent upon the concentration of TP (Schindler 1977). Because TP and chlorophyll *a* are highly correlated in lakes (Nicholls and Dillon 1978), chlorophyll *a* should also be correlated with TDS. I examined this hypothesis with data collected by Prepas and Trew (1983) for 25 lakes located over a large region (7×10^4 km^2) in central Alberta, in the drainage basins of three major river systems (Athabasca, Beaver, and North Saskatchewan rivers). In these lakes $\bar{z}$ ranged from 2.4 to 19 m, summer epilimnetic TDS from 128 to 1545 mg/L, and average summer chlorophyll *a* collected from the trophogenic zone (down to 1% surface-penetrating irradiance) from 1.7 to 150 mg/m^3. These lakes satisfy both of Ryder's conditions under which TDS should be an important parameter. However, there was no relationship between TDS and chlorophyll *a* in these lakes (Fig. 1). There was also no relationship between mean summer epilimnetic TDS and TP ($n = 31$, $r^2 = 0.00$, $P = 0.77$ on a log−log scale), whereas TP and chlorophyll *a* were highly correlated (Prepas and Trew 1983). Thus TDS was not a good predictor of phytoplankton biomass, as measured by chlorophyll *a*, in these lakes.

None of the 25 lakes were located on the Precambrian Shield, whereas both on-shield and off-shield lakes were included in the previous studies which showed a positive correlation between TDS and productivity (Table 1). The lakes in each of the previous studies were therefore divided into two groups, on-shield and off-shield, to determine whether TDS was correlated with productivity within each group. The division between on-shield and off-shield lakes was set at 100 mg TDS/L (Rawson 1951). Lake location was not used to classify lakes because a lake can be located in a different region than its major source of water. Both on- and off-shield lakes cover a large region, i.e. the lakes used by Ryder (1965) and Matuszek (1978) extend from the Northwest Territories (north of Alberta) to Ontario, and from Alberta to Ontario, for the two regions, respectively, and the lakes analyzed by

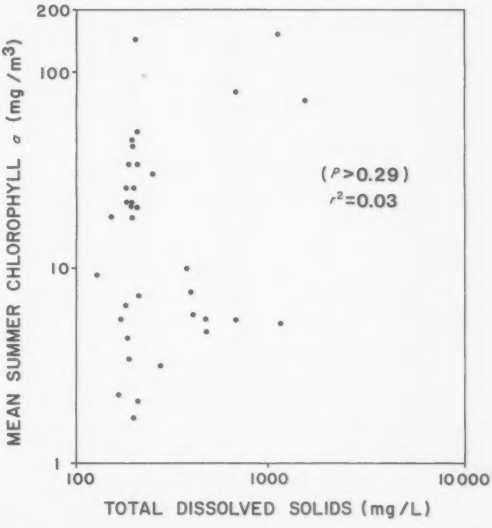

FIG. 1. Relationship between summer chlorophyll *a* within the trophogenic zone and total dissolved solids within the epilimnion in 25 off-shield lakes in central Alberta. There are 35 points because six lakes were studied for 2 yr and two of those lakes were double-basined. Data from Prepas and Trew (1983).

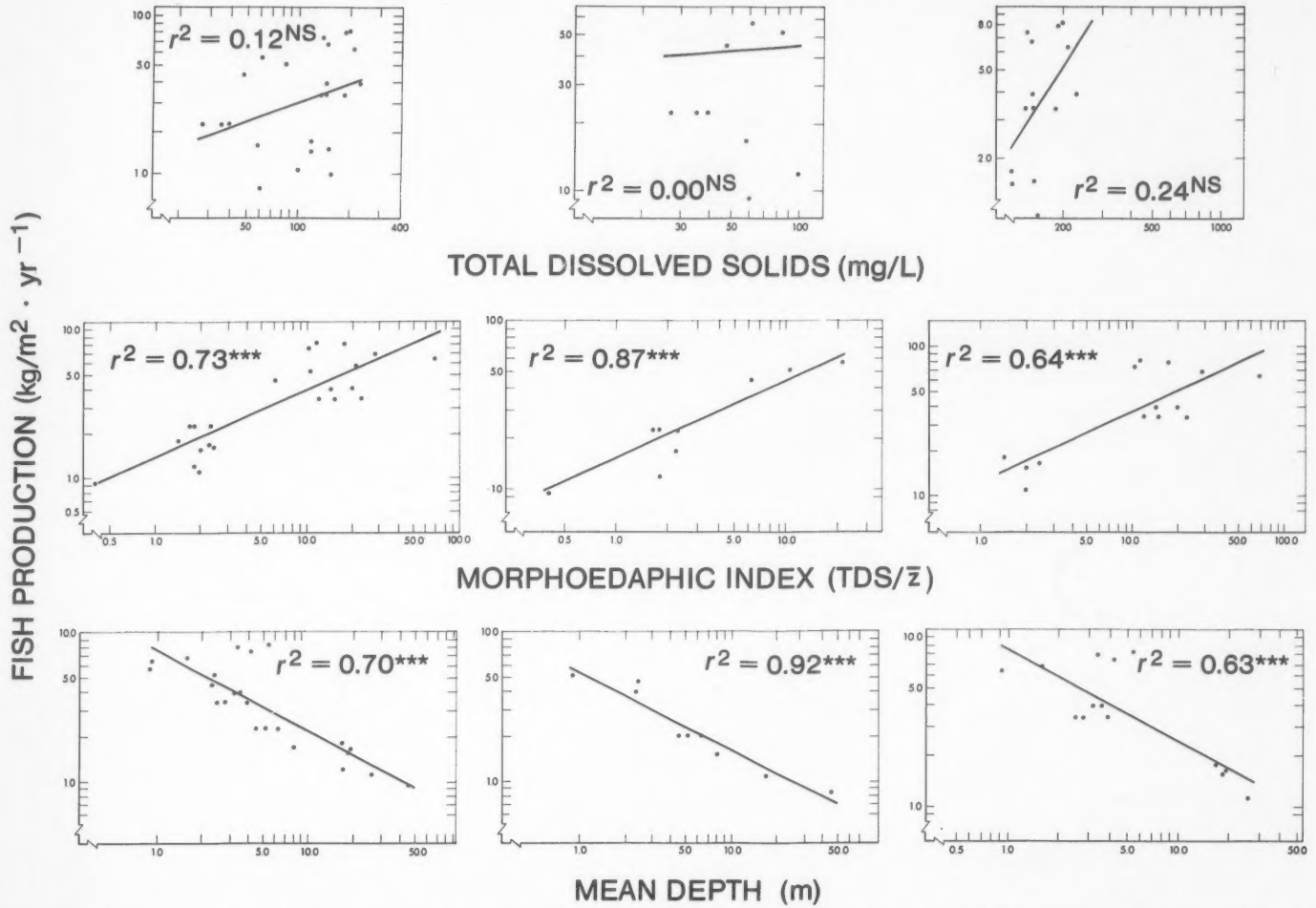

FIG. 2. Relationship between fish production and total dissolved solids (TDS), the TDS:mean depth ($\bar{z}$) ratio or morphoedaphic index, and $\bar{z}$. All lakes are included in the first graph in each row, whereas the second and third graphs, respectively, include only those lakes on and off the Precambrian Shield. Data are from Ryder (1965). Significant correlations are indicated by *** ($P < 0.001$), nonsignificant correlations by ns ($P > 0.05$).

Hanson and Leggett (1982) include the same territory plus the northern United States and northern Europe. Even though the range of TDS is reduced when a data set is divided into on-shield and off-shield classifications, these groupings still cover a broad enough range of nutrient concentrations that TDS should be a useful parameter for predicting lake productivity (Ryder et al. 1974; Ryder 1982). However, there was no significant positive relationship between TDS and fish production, TDS and fish catch, TDS and plankton biomass, or TDS and benthic biomass in either on-shield or off-shield lakes. Moreover, in nine cases the correlation coefficients approached zero and there was one significant negative correlation (Table 1). Therefore the previously observed positive correlations between TDS and these indices were only indicators of the differences between on-shield and off-shield lakes.

Ryder (1965) observed that the relationship between fish production and TDS was not significant ($P > 0.05$, Fig. 2). However, he found the correlation between $\bar{z}$ and fish production was highly significant and that this relationship was marginally improved when the MEI was used ($r^2 = 0.73$ as compared to 0.70, Fig. 2). When the lakes were separated into on-shield and off-shield, $\bar{z}$ was a better predictor than MEI for on-shield lakes ($r^2 = 0.92$ as compared to 0.87) whereas for off-shield lakes MEI was slightly better than $\bar{z}$ ($r^2 = 0.64$ as compared to 0.63, Fig. 2). This suggests that there is no reason to use the TDS:$\bar{z}$ ratio as opposed to $\bar{z}$ to predict fish production.

I conclude that TDS does not predict productivity for either on-shield or off-shield lakes, but only indicates productivity differences between them. Furthermore no new information is gained when the TDS:$\bar{z}$ ratio is used rather than just $\bar{z}$. Therefore TDS does not seem to be a useful parameter in empirical models which predict lake productivity.

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HANSON, J. M., AND W. C. LEGGETT. 1982. Empirical prediction of fish biomass and yield. Can. J. Fish. Aquat. Sci. 39: 257–263.

HARTMANN, J., AND W. NÜMANN. 1977. Percids of Lake Constance, a lake undergoing eutrophication. J. Fish. Res. Board Can. 34: 1670–1677.

MATUSZEK, J. E. 1978. Empirical predictions of fish yields of large North American lakes. Trans. Am. Fish. Soc. 107: 385–394.

NICHOLLS, K. H., AND P. J. DILLON. 1978. An evaluation of phosphorus–chlorophyll–phytoplankton relationships for lakes. Int. Rev. Gesamten Hydrobiol. 63: 141–154.

OGLESBY, R. T. 1977. Relationships of fish yield to lake phytoplankton standing crop, production, and morphoedaphic factors. J. Fish. Res. Board Can. 34: 2271–2279.

PREPAS, E. E., AND D. O. TREW. 1983. Evaluation of the phosphorus–chlorophyll relationship for lakes off the Precambrian Shield in western Canada. Can. J. Fish. Aquat. Sci. 40: 27–35.

RAWSON, D. S. 1951. The total mineral content of lake waters. Ecology 32: 669–672.

1960. A limnological comparison of twelve large lakes in Northern Saskatchewan. Limnol. Oceanogr. 5: 195–211.

RYDER, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214–218.

1982. The morphoedaphic index — use, abuse, and fundamental concepts. Trans. Am. Fish. Soc. 111: 154–164.

RYDER, R. A., S. R. KERR, K. H. LOFTUS, AND H. A. REGIER. 1974. The morphoedaphic index, a fish yield estimator — review and evaluation. J. Fish. Res. Board Can. 31: 663–688.

SCHINDLER, D. W. 1977. Evolution of phosphorus limitation in lakes. Science 195: 260–262.

WILLEMSEN, J. 1977. Population dynamics of percids in Lake Ijssel and some smaller lakes in the Netherlands. J. Fish. Res. Board Can. 34: 1710–1719.

Consideration of the Stable Age Distribution Assumption in "Analytical" Yield Models

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SINCLAIR, M., R. O'BOYLE, AND T. D. ILES. 1983. Consideration of the stable age distribution assumption in "analytical" yield models. Can. J. Fish. Aquat. Sci. 40: 95–101.

The implications on the "analytical" yield model of deviations from the stable age distribution were investigated for stocks of five species with a range of life history characteristics, these being Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), Atlantic herring (*Clupea harengus harengus*), and Atlantic

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mackerel (*Scomber scrombus*). Recruitment variability for the stocks considered ranged from 21% for pollock to 104% for haddock. The comparison of the growth rates at age for the five species showed the expected continuum in relative growth rates from cod to mackerel. With the population in a stable age distribution without fishing there is also a continuum from cod to mackerel in the manner in which age-specific production decreases through the life span. It is thus to be expected that deviations from the stable age distributions for mackerel would have a much greater impact on population production than would a similar deviation for cod. Also, species whose growth rates decrease more rapidly with age tend to have a higher recruitment variability. To demonstrate the implications of deviations from the stable age distribution on the accuracy of model output, MSY yields (that would have been generated given historical estimates of population numbers-at-age) were compared to estimates of annual population production. Cod and pollock production deviate relatively little from the "analytical" model predictions. In contrast, annual production for haddock, herring, and mackerel deviate markedly from MSY yields as the age composition deviates in each direction from the stable age distribution. The analysis suggests that for some species the "analytical" model may contribute to growth overfishing.

Key words: "analytical" yield models, stable age distribution, growth overfishing

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Le présent rapport porte sur une étude de l'incidence des déviations de la répartition stable des âges sur le modèle analytique du rendement de cinq espèces de poissons ayant des cycles vitaux différents, soit la morue de l'Atlantique (*Gadus morhua*), l'aiglefin (*Melanogrammus aeglefinus*), la goberge (*Pollachius virens*), le hareng de l'Atlantique (*Clupea harengus harengus*) et le maquereau bleu (*Scomber scombrus*). La variabilité du recrutement des stocks étudiés varie de 21 % pour la goberge à 104 % pour l'aiglefin. La comparaison des taux de croissance à un âge donné pour les cinq espèces confirme le continuum des taux de croissance relatifs, de la morue au maquereau. Ce continuum est aussi présent dans la production d'une classe d'âge, qui diminue au cours de la vie, quand la répartition des âges de la population est stable et en l'absence de pêche. On doit donc s'attendre à ce que les déviations des répartitions stables des âges du maquereau aient une plus grande incidence sur la production de la population qu'une déviation semblable pour la morue. De plus, les espèces dont le taux de croissance diminue plus rapidement en fonction de l'âge ont tendance à avoir un taux plus élevé de variabilité du recrutement. Afin de démontrer l'incidence des déviations de la répartition stable des âges sur la précision du modèle, on a comparé les rendements optimaux soutenus (qui auraient été obtenus étant donné les estimations passées du nombre à un âge donné) aux estimations de la production annuelle d'une espèce. La production de morue et de goberge dévie peu des prévisions du modèle analytique. Par contre, la production annuelle d'aiglefin, de hareng et de maquereau dévie nettement des ROS quand la répartition des âges dévie dans chaque direction de la répartition stable des âges. Cette analyse porte à croire que, pour certaines espèces, le modèle analytique peut contribuer à une surpêche par rapport à la croissance.

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MOST models dealing with life history tactics assume that the members of the populations are in a stable age distribution (e.g. Fisher 1930; Cole 1954). Surprisingly the implications of relaxing this assumption have not been worked out (Stearns 1976). The exploited fish population "analytical" yield model (Baranov 1918), and its derivations (Thompson and Bell 1934; Beverton and Holt 1957), which allow estimation of sustainable yield as a function of fishing effort and gear selectivity-at-age, also assume a stable age distribution. Because the "analytical" models are routinely used in fish stock assessments to provide management advice, it is of some importance that the basic assumptions of the model are adequately met for natural populations. In addition, it is important that the biological limitations be evaluated because bioeconomic studies, both theoretical and applied, use such yield models as a starting point in the development of fisheries economic models (Clark 1976). It is the aim of this note to evaluate critically the implications on the "analytical" yield model of deviations from the stable age distribution.

The model and its application — The "analytical" yield models consider the catch obtained from one year-class, or

TABLE 1. Management units and the coefficient of variation of recruitment for the five fish stocks considered (4T, 4X, 4WX, 3–6, 4VWX-5 are geographical areas defined under the Northwest Atlantic Fisheries Organization).

Management unit	Time span of cohort analysis	Recruitment C.V., %	Relative confidence in cohort analysis
Cod 4T[a]	1950–77	40	Good
Haddock 4X[b]	1962–78	104	Good
Herring 4WX[c]	1968–79	86	Medium–good
Mackerel 3–6[d]	1968–77	77	Poor
Pollock 4VWX-5[e]	1973–78	21	Poor

[a]Gray (1979) and Lett (1978).
[b]O'Boyle (1980).
[c]Sinclair and Iles (1980).
[d]Maguire (1979).
[e]Cleary (1980).

cohort, throughout its life. It follows that under steady state conditions (i.e. stable age distribution) the annual catch from the overall population under a given fishing strategy equals the catch that can be taken from a single cohort throughout its life under the same strategy. This has been called the "principle of equivalence." Thus annual yield at constant recruitment can be maximized by maximizing the following relationship for a single cohort,

$$Y = \int_{t=1}^{n} F_t \cdot N_t \cdot W_t \cdot dt$$

in which Y is the annual yield, F_t is the instantaneous fishing mortality, N_t the abundance of the cohort at age t, and W_t the fish weight at age t. Beverton and Holt (1957) identified separately the age at recruitment to the population and the age of availability of the cohort to the fishing gear. In practical terms this allowed one to evaluate the effect of varying fishing gear selectivity, as well as fishing effort, on the sustainable yield. In the original formulation, as well as in most of the subsequent applications, N_t is a simple function involving constant recruitment, constant natural mortality at age, and variable fishing mortality at age. W_t was described empirically (Thompson and Bell 1934) or by using an appropriate growth equation (Beverton and Holt 1957). In the yield per recruit derivation (Beverton and Holt 1957), sustainable yield per recruit (again at constant recruitment and a stable age distribution) can be predicted as a function of various fishing strategies, involving both the total fishing effort (i.e. fishing mortality, F) and the manner in which it is distributed over ages. It is this latter derivation that is routinely used in fish stock assessments. The fishing mortality that predicts either maximum sustainable yield per recruit (F_{MSY}), or an alternate sustainable yield for a different management strategy, such as $F_{0.1}$ yield (Gulland 1968; Gulland and Boerema 1973) for a given gear selectivity-at-age, is the model output of interest to management.

To generate biological advice on catch quotas for a fish stock on a yearly basis, assessment biologists apply the fishing mortalities-at-age, which predict MSY or $F_{0.1}$ yield, to the present stock abundance-at-age estimates derived from cohort analysis (Pope 1972). The summation of the calculated removals-at-age times the weights-at-age provide an estimate of the catch quota in tons [the total allowable catch (TAC)] under the chosen management strategy (such as $F_{0.1}$ yield or MSY).

The key point here is that in the application of the "analytical" model, an optimal fishing mortality, defined under the assumption of a population producing with a stable age distribution, is applied against a population which may not be appropriately distributed. It is important to note that although the yield per recruit derivation of the "analytical" model permitted its application under variable recruitment, it did not remove the constraint of the stable age distribution.

In this note the relative importance of deviations from the stable age distribution constraint, due both to recruitment variability and the decline in growth rate with age, are evaluated for five species with a range of life history characteristics [Atlantic cod (*Gadus morhua*), pollock (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), Atlantic herring (*Clupea harengus harengus*), and Atlantic mackerel (*Scomber scrombus*)].

Materials and methods — The population production characteristics of five Canadian Atlantic coast fish stocks were examined. These stocks were 4T cod, 4X haddock, 4VWX-5 pollock, 3–6 mackerel, and 4WX herring. Exploitation of these stocks is presently being managed through the use of some variant of the "analytical" yield model.

Beginning of year recruitment and midyear weight-at-age estimates were obtained for each stock from recent CAFSAC (Canadian Atlantic Fisheries Scientific Advisory Committee) Research Documents, which are referenced in Table 1. The data sets varied considerably in length. That for cod covered 28 yr whereas that for pollock only 6 (Table 1).

Recruitment was always taken as the population numbers present in the earliest age-group to be exploited by the fishery. In practice, this is the top row of the population matrix from a sequential population analysis, such as cohort analysis (Pope 1972).

Annual growth-at-age estimates were calculated using the weight-at-age matrices available in the CAFSAC reports indicated above. First, an overall estimate of weight-at-age was obtained for each stock by averaging the empirically

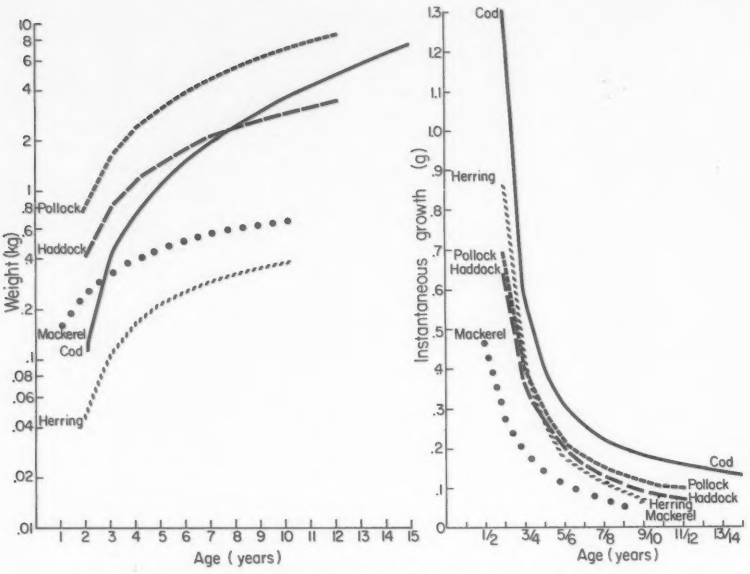

FIG. 1. Weights-at-age and growth rates-at-age for the five stocks considered.

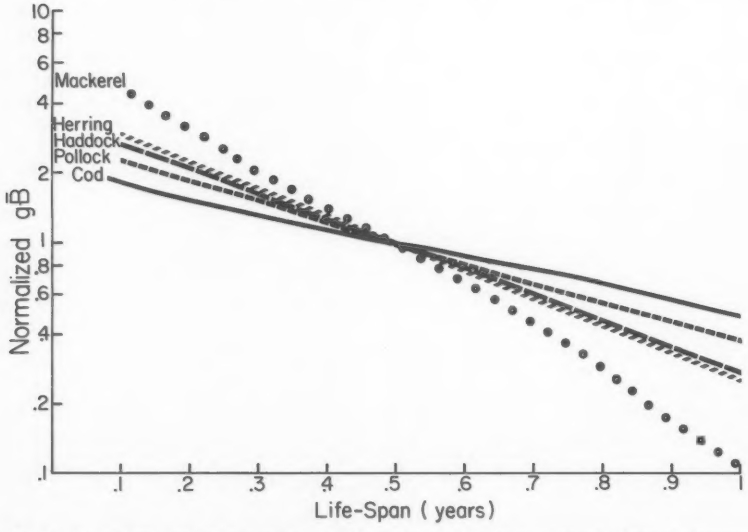

FIG. 2. Normalized production in relation to life span for the five stocks considered. Cross-age biomass ($\bar{B}$) is the average of consecutive biomasses-at-age (weight-at-age times numbers-at-age in the stable size distribution) and g is the instantaneous growth rate.

derived matrices over years. Smoothed weight-at-age estimates were then obtained by fitting the averaged data with the von Bertalanffy growth model, except in the case of pollock where a linear model proved more appropriate. In no case was the R^2 less than 0.99. Weight-at-age estimates were calculated for each species using these equations. Mean annual instantaneous growth rates-at-age were calculated by,

$$g = \log_e W_{t+1} - \log_e W_t$$

where W_t and W_{t+1} are the weights-at-age (Ricker 1975).

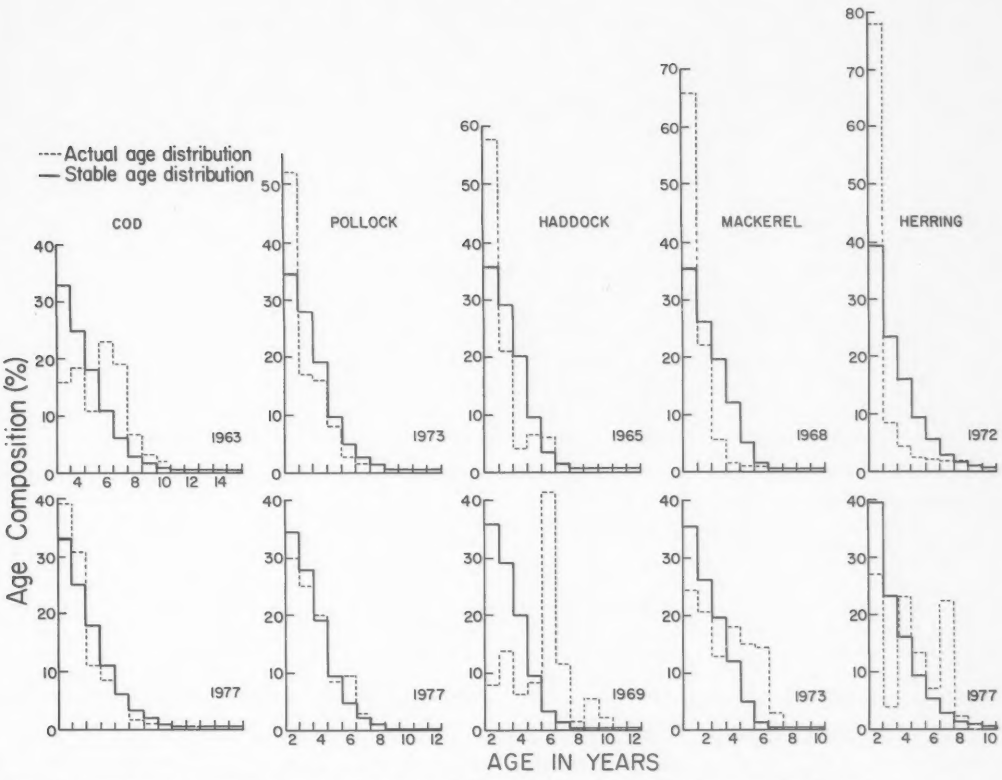

FIG. 3. Comparison of examples of actual population age distributions to the stable age distribution for the five stocks.

Annual population production was estimated by

$$P = \sum(W_{t+1} - W_t) \cdot N_{t+1}$$

where N_{t+1} is the cohort analysis estimate of numbers-at-age $t+1$ (January 1). Maximum sustainable yield and $F_{0.1}$ yield in numbers were estimated by applying the appropriate fishing mortality, derived from the "analytical" yield model, to the population estimates by year for the five species (Table 1). Yield in weight was estimated using the mean weights-at-age. The partial recruitment patterns and the natural mortality rates were those used in the various stock assessments referenced in Table 1.

Results and discussion — Two factors influence the degree of departure from the stable age distribution: recruitment variability, coupled with the decrease in growth rate at age. Both factors vary considerably between species. The recruitment variability for several species fished off eastern Canadian waters which are managed using the "analytical" model are shown in Table 1. The coefficients of variation range from 21% for pollock to 104% for haddock. The growth rates as well as the weights-at-age for five of these species are shown in Fig. 1. The key point here is that certain species continue to grow relatively rapidly at older ages, particularly cod. At the other extreme mackerel growth rates decrease rapidly with age. The expected continuum in relative growth rates from cod to mackerel is clear.

With the population in the stable age distribution without fishing, there is also a continuum from cod to mackerel in the manner in which age-specific production decreases through the life span (Fig. 2). Cross-age biomass ($\bar{B}$) is the average of consecutive biomasses at age (weight-at-age times numbers-at-age in the stable age distribution). The stable age distributions were estimated assuming constant recruitment and natural mortality-at-age using the data sources indicated in Table 1. Production at various portions of the life span was normalized by the value at the 50% point of the age span considered to facilitate between species comparisons of the life history growth strategies. It is evident that deviations from the stable age distributions for mackerel would have a much greater impact on population production than would a similar deviation for cod. Therefore, the assumption of adherence to the stable age distribution for the analytical yield models can

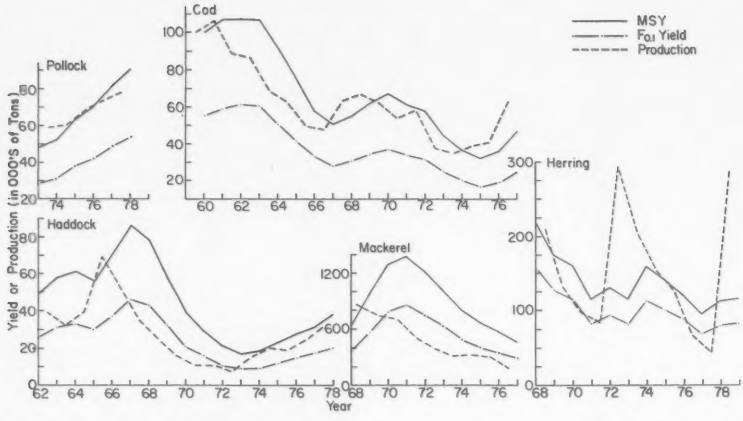

FIG. 4. Comparison of MSY and $F_{0.1}$ yield estimates to annual production calculated using historical population-at-age estimates.

be expected to vary between species. Cod and pollock would probably be little influenced by deviations, but haddock, herring, and mackerel progressively more influenced.

It is unfortunate in terms of the model, but perhaps related in evolutionary terms, that the species whose growth rates decrease more rapidly with age also have a higher recruitment variability. Examples of the deviation of the age distribution for each species from the stable age distribution at F_{MSY} (generated using the more recent gear selectivity-at-age distribution for the specific fisheries; sources in Table 1) are shown in Fig. 3. In the lower half of the figure extreme deviations towards older ages in the population are shown, whereas examples of extreme deviations towards younger age-classes are shown in the upper half. Haddock and herring show more dramatic departures from stable age distribution. The effects on population production are compounded when growth rates at age (Fig. 2) are also considered.

To demonstrate the implications of these deviations from the stable age distribution on the accuracy of model output, the MSY yield that would have been generated given the estimated population numbers-at-age and the observed weights-at-age are compared to an estimate of annual population production (Fig. 4). We stress that the respective fish stocks were not managed at MSY or $F_{0.1}$ yield over these time periods, but that the historical fluctuations in population structure provide a realistic empirical data base for which the importance of deviations from the stable age distribution can be explored.

It is the between-species differences in the relative distributions of MSY yield and annual population production that are of interest. Cod and pollock production deviate relatively little from the "analytical" model predictions as the age composition deviates in each direction from the stable age distribution. In contrast, annual production for haddock, herring, and mackerel deviate markedly from MSY yield. For example, as the exceptional 1963 haddock year-class progresses through the life span, the population production deviates progressively from MSY yield advice that would have been generated using the "analytical" model. A similar distribution is observed for the herring example. As the age composition was skewed towards older ages in the early 1970s and during 1976 and 1977, population production was much lower than is predicted using the "analytical" model which assumes that the population biomass is distributed through the life span in the stable age distribution. The situation is worse for mackerel. Even slight deviations from the stable age distribution markedly affect the accuracy of the model output. These results suggest that the "analytical" model would consistently overestimate the production capacity of the stock. The biologically more conservative $F_{0.1}$ yield, a frequently adopted management strategy, is also often higher than the short-term production capacity of several of the populations.

The continuum (for the five species considered here) in the distribution of $g\bar{B}$ through the life span (Fig. 2) is roughly paralleled by their degree of deviation from the MSY yield predictions (Fig. 4). The between-species recruitment variability modifies the continuum somewhat. Pollock with the lowest year-class strength variability does somewhat better than cod, whereas haddock, with the highest variability, fares worse than herring. An intermediate recruitment variability for mackerel, however, does not change its relative position.

The conclusion of this analysis is that the assumption of the stable age distribution in the "analytical" yield model is a rigorous one, but that there is a range in sensitivity according to the growth strategy and recruitment variability of the fished species. It may be no accident that haddock, herring, and mackerel are frequent examples of stocks that have been overfished under management regimes using the "analytical" model to generate TACs. Cushing (1975) has stated that the "analytical" model has resolved the growth overfishing problem. This analysis suggests rather that for some species or stocks the "analytical" model may contribute to growth overfishing.

BARANOV, F. I. 1918. On the question of the biological basis of fisheries. Nauch. Issled. Ikhtiol. Inst. Izv. 1: 81–128. (In

Russian)
BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. U.K. Min. Agric. Fish. Fish. Invest. (Ser. 2) 19: 533 p.
CLARK, C. W. 1976. Mathematical bioeconomics, the optimal management of renewable resources. Wiley-Interscience, New York, NY. 352 p.
CLEARY, L. 1980. Assessment of 4VWX-5-6 pollock. CAFSAC Res. Doc. 80/1.
COLE, L. C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29: 103–137.
CUSHING, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, London. 278 p.
FISHER, R. A. 1930. The genetical theory of natural selection. Dover, New York.
GRAY, D. F. 1979. The 1979 assessment of cod in Divisions 4T and 4Vn (Jan.–Apr.). CAFSAC Res. Doc. 79/21.
GULLAND, J. A. 1968. The concept of the marginal yield from exploited fish stocks. J. Cons. Perm. Int. Explor. Mer 32: 256–261.
GULLAND, J. A., AND L. K. BOEREMA. 1973. Scientific advice on catch levels. Fish. Bull. 71: 325–335.
LETT, P. F. 1978. A comparative study of the recruitment mechanisms of cod and mackerel. Ph.D. thesis, Dalhousie Univ., Halifax, N.S. 125 p.
MAGUIRE, J. J. 1979. An analytical assessment of SA 3–6 mackerel with information from egg and larval surveys. CAFSAC Res. Doc. 79/46.
O'BOYLE, R. N. 1980. ICNAF Division 4X haddock January 1980 status report. CAFSAC Res. Doc. 80/2.
POPE, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Bull. Int. Comm. Northw. Atl. Fish. 9: 65–74.
RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.
SINCLAIR, M., AND T. D. ILES. 1980. 1979 4WX herring assessment. CAFSAC Res. Doc. 80/47.
STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3–47.
THOMPSON, W. F., AND F. H. BELL. 1934. Biological statistics of the Pacific halibut fishery. (2) Effect of changes in intensity upon total yield and yield per unit of gear. Rep. Int. Fish. [Pacific Halibut] Comm. 8: 1–49.

Potentiated Sulfonamide Therapy of Enteric Redmouth Disease[1]

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BULLOCK, G. L., G. MAESTRONE, C. STARLIPER, AND B. SCHILL. 1983. Potentiated sulfonamide therapy of enteric redmouth disease. Can. J. Fish. Aquat. Sci. 40: 101–102.

Effective control of enteric redmouth disease was obtained during artificial infection of rainbow trout (*Salmo gairdneri*) and in natural outbreaks in rainbow trout and chinook salmon (*Oncorhynchus tshawytscha*) with a potentiated sulfonamide, Ro5-0037, a combination of five parts sulfadimethoxine and one part ormetoprim. Treatment was given at the rate of 50 mg/kg of fish for 5 d.

Key words: potentiated sulfonamide, enteric redmouth, therapy, salmonids

BULLOCK, G. L., G. MAESTRONE, C. STARLIPER, AND B. SCHILL. 1983. Potentiated sulfonamide therapy of enteric redmouth disease. Can. J. Fish. Aquat. Sci. 40: 101–102.

On a réussi à éliminer efficacement la maladie bactérienne de la bouche rouge à la suite de l'infection artificielle de la truite arc-en-ciel (*Salmo gairdneri*) et du déclenchement naturel de la maladie chez la truite arc-en-ciel et le saumon quinnat (*Oncorhynchus tshawytscha*), avec du sulfonamide potentialisé, Ro5-0037, qui consiste en cinq parties de sulfadiméthoxine et une partie d'ormétoprime. Le traitement a été administré à raison de 50 mg/kg de pesanteur, pendant 5 jours.

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[1]The U.S. Fish and Wildlife Service enters into cooperative agreements with interested companies to conduct essential studies required for the registration of priority chemicals and drugs with fishery and wildlife uses. Co-authorship in a publication does not imply agency endorsement of company product.

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THE potentiated sulfonamide Ro5-0037 is a combination of five parts sulfadimethoxine and one part ormetoprim (a diamino-pyrimidine) that has previously been shown to control furunculosis when fed daily for 2 wk at 50 mg/kg of fish (Bullock et al. 1974). Although treatment was effective, Ro5-0037-depletion studies showed that 10–12 wk were required for the drug to clear muscle and skin tissues. Because the long retention time would require that fish be held at least 3 mo after treatment before being stocked or consumed, a shorter term feeding trial was conducted. When fed for just 5 d, Ro5-0037 cleared tissues within 5 wk. Accordingly, field studies were undertaken to evaluate the efficacy of 5-d treatments for control of furunculosis. Because in vitro tests showed that the enteric redmouth (ERM) organism *Yersinia ruckeri* was sensitive to Ro5-0037, we also initiated an evaluation of Ro5-0037 for ERM. Results of the ERM tests are described in this report, and the furunculosis studies will be reported elsewhere.

Materials and methods — A laboratory efficacy test for control of ERM was performed in four 114-L tanks, each containing 100 rainbow trout (*Salmo gairdneri*) weighing 7–9 g each. Trout in each tank were challenged by first draining the water then exposing them for 90 s to 1 L (plus a very small amount of residual water) of a 24-h brain heart infusion culture of *Y. ruckeri* containing 1×10^9 colony-forming units/mL as determined by the method of Miles and Misra (1938). Water was then turned on and beginning 24 h after challenge, trout in two tanks were fed a diet containing 50 mg of Ro5-0037 · kg of fish^{-1} · d^{-1} for 5 d whereas controls were fed an identical but nonmedicated diet. Medicated diet was prepared by coating No. 4 diet crumbles with a 30% Ro5-0037 soybean meal premix suspended in vegetable oil.

Additional efficacy tests were carried out with 1000 medicated and 1000 nonmedicated rainbow trout at a federal hatchery in North Carolina and with 500000 medicated and 500000 nonmedicated fall chinook salmon (*Oncorhynchus tshawytscha*) at a state hatchery in Oregon. Medicated diets were prepared at each location using the 30% Ro5-0037 premix. Feed samples were sent to Hoffmann-La Roche, Inc. for determination of Ro5-0037 content. The presence of *Y. ruckeri* was confirmed at each hatchery and epizootics were in progress before Ro5-0037 treatment began. Mortality records were kept on all lots of salmonids during treatment and for 2 wk afterward. In all field tests *Y. ruckeri* was confirmed as the cause of mortality.

Results and discussion — Enteric redmouth was effectively controlled in both the laboratory test and the hatchery trial in North Carolina. Treated trout in the laboratory test sustained 5% mortality, whereas 75% mortality occurred among nontreated trout. Treated trout at the North Carolina hatchery suffered 5% mortality, whereas 15% of the nonmedicated trout died. Results from both trials were significant at the 95% confidence limits with the z-test (Snedecor and Cochran 1978). At first, Ro5-0037 treatment of salmon in Oregon appeared to be ineffective because nonmedicated trout suffered 3.7% mortality, but 8.5% of treated salmon died. We later found that these salmon were also infected with the kidney disease bacterium *Renibacterium salmoninarum* and suffered recurrent bacterial gill disease. The cause of mortality was not ERM because bacteriological culturing of salmon kidney tissue following Ro5-0037 treatment and observation period showed 60% of 160 untreated fish with ERM; however, *Y. ruckeri* was present in only 7% of 600 treated salmon examined. Analysis of samples showed all medicated diets contained 84–93% of the calculated amount of Ro5-0037.

Results obtained in this study indicated that the 5-d treatment would control ERM. However, effective use of antibacterial therapy requires the drug be used at the correct level, that it begin as soon as possible when an epizootic is recognized, and that the treated population be free of other microbial pathogens. The presence of renibacterial kidney disease and bacterial gill disease in test salmon in Oregon complicated our evaluation of the Ro5-0037 treatment. Because bacteriological examination showed only 7% of treated salmon was infected with *Y. ruckeri* whereas 60% of nontreated salmon was infected, clearly indicates that salmon were not dying from enteric redmouth disease. Additional efficacy tests will be carried out to obtain data for clearance by the Food and Drug Administration of Ro5-0037 for control of ERM. If approved, Ro5-0037 will represent the first drug cleared in the United States for treating ERM.

BULLOCK, G. L., H. M. STUCKEY, D. COLLIS, R. L. HERMAN, AND G. MAESTRONE. 1974. In vitro and in vivo efficacy of a potentiated sulfonamide in control of furunculosis in salmonids. J. Fish. Res. Board Can. 31: 75–82.

MILES, A. A., AND S. S. MISRA. 1938. The estimation of the bacteriocidal power of the blood. J. Hyg. 38: 732–749.

SNEDECOR, G. W., AND W. G. COCHRAN. 1978. Statistical methods. The Iowa State University Press, Ames, IA. 593 p.

BOOK REVIEWS/COMPTES RENDUS

Principles of Benthic Marine Paleoecology. *Arthur J. Boucot with contributions by Robert S. Carney. Academic Press Canada, Don Mills, Ont. 1981. 463 p. $86.45.*

The authors of this volume are to be lauded for their timely endeavor to apply methods and theories of modern ecology to those of paleocommunity ecology. The perspective emphasizes the influences of external factors and subsequent environmental interpretation; as such, the book is a must for the shelves of every modern benthic ecologist. For the paleoecologist faced with a static assemblage, there is a much-needed documentation of those phenomena that allow recognition of principal environmental parameters. The juxtaposition of modern and ancient examples is useful although occasionally ideal lessons in environmental reconstruction are omitted.

The initial chapters on environmental variables are particularly comprehensive and the literature review spanning a wide variety of ecosystems is remarkable. The fourth chapter, in addition to being somewhat easier to read, is replete with descriptions of the establishment and maintenance of community patterns. Postmortality processes, the bane of the paleoecologist, are given no undue emphasis. The final chapter is a particularly enlightening discourse on trace fossils by Robert Carney; it is an indispensible guide to the bewildering array of "ichnias" in which paleontological psychologists appear to delight. This inclusion is one more step in establishing the importance of ichnology in the art of paleoenvironmental interpretation.

Two minor faults of the book lie more with the publisher. Omission of numerous important references to recent material testifies to the protracted nature of preparation and publication in this day. Second, the number and size of the figures are decidedly excessive; there are as many figures and tables as there are pages of text. Most students would gladly trade the graphics for a reduced price tag. Indeed, this excellent volume should be coveted by students and practitioners of the ancient and modern alike.

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Journal of Freshwater Ecology. *Volume 1, Numbers 1–3. Edited by J. A. Kawatski. Oikos Publishers, Inc., La Crosse, Wisconsin. Subscriptions — $35/volume (library and institutions); $25 (individuals).*

The *Journal of Freshwater Ecology* is new, attempting to address two problems inherent in most scientific journals: high costs (of reproduction and subscriptions) and slow turnaround time (between submission and publication). This journal, edited by J. A. Kawatski, uses direct copy photography to minimize both problems. Direct copy photography is faster than typesetting but has the disadvantages of having articles with different size and style of typescript and less flexible format. However, these esthetic considerations are secondary to the primary purpose; that of information transfer. Those seeking scientific information do not care to wait for information to be packaged in an esthetically pleasing, slick way; they simply want valid, credible results reasonably quickly. However, the integrity of the science is just as important or more important as speed of dissemination and low cost. If the standards for the journal are not high, low cost and rapid turnaround loose their worth.

Because of the reproduction method, the first impression of the journal is one of being "unpolished;" however, this is no inherent disadvantage. But what the more "polished" journals appear to have is an attention to detail which goes along with the better appearance. The *Journal of Freshwater Ecology* indicates that abbreviations and symbols should match the AIBS Style Manual, but, nevertheless, several examples were noted that did not conform to this source: there are different journal abbreviations and inconsistent bibliographic reference styles.

The content of the Journal is as wide as the name might suggest; there is a broad range of topics although the emphasis is, as might be expected, biology. In the first three issues, there are a number of articles on limnology and on stream benthos plus a variety of other topics: production, statistics, and methodological papers; even a paper resurrecting the specter (assumed to be long dead) of carbon dioxide limitation of phytoplankton growth. Many of the papers are descriptive (as opposed to experimental) in nature, but several useful and interesting data sets and interpretations are presented. Because of the variety of material, positive or negative reactions to specific articles are generally based on one's own area of specialty, but articles by Effler et al. and Rosen (both in Vol. 1, No. 2) appealed to me as sound, interesting work.

In view of the present state of technology, present and future trends in transfer of scientific information should be considered. The basic structure of scientific journals has changed little in the past 100 years. Other than proliferation of new journals into more specialized areas and provision of more detailed information, journals' structure and format remain basically unaltered. Considering the changes in other areas of information dissemination, the lack of change is very surprising, perhaps reflecting the conservative nature of science. However, changes will likely be imposed on journals as the technological revolution in information transfer gains momentum. Many agencies and laboratories have computerized information retrieval systems for access to new information (which has reached an unprecedented volume). Can electronic and/or computer-assisted dissemination of journal articles be very far in the future? Certainly, it would be logical

strategy for progressive journals in efforts to reduce costs and turnaround time.

Does the *Journal of Freshwater Ecology* succeed in its intentions of shorter turnaround time and reasonable cost? In terms of turnaround time, there is no basis of judgment; in contrast to many other journals, no submission date and acceptance date are included with the articles. The subscription cost, taken at face value, is very reasonable, but cost per page is a better criterion. For three other journals, the 1981 cost per page was calculated: *Limnology and Oceanography*, *Water Research*, and *Canadian Journal of Fisheries and Aquatic Sciences* range from 2.6 to 4.0¢ per page. In comparison, the *Journal of Freshwater Ecology* cost per page is 7.4¢. Only three (of the six) issues of the first volume appeared in 1981, so the comparison is difficult to make.

If this journal does not care to demonstrate an improved turnaround time and if its value for money and quality do not compare favorably with established journals in the field, the journal does not seem to be succeeding in its stated objectives.

Undertaking the creation of a new journal is a major endeavor; there are obvious start-up difficulties. It would appear that more effort should be made to achieve the stated goals of the journal and to improve its quality before it is considered to be successful.

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(R421)

Books received/Livres reçus
September/septembre 1982

Philopatry, inbreeding, and the evolution of sex. *William M. Shields. State University of New York Press, Albany, NY. 1982. ix + 245 p. Cloth $49.00 (U.S.), paper $16.95.* The author's initial question of why so many organisms disperse relatively short distances before settling to breed led to other questions regarding breeding. He has drawn on theory and data from the fields of behavior, ecology, and genetics in his attempt to provide a comprehensive evolutionary framework. [R448]

Progrès dans les traitements par le froid des poissons/Advances in the refrigerated treatment of fish. *Edité par Institut international de Froid/Issued by International Institute of Refrigeration, Paris, France. 1981. 637 p. 190 FF (hard cover).* The International Institute of Refrigeration meeting held in Boston August 3–6, 1981, provided an occasion to survey the present state of "Advances in the refrigerated treatment of fish, especially underutilized species." This book contains the full texts of the presented papers and a summary of the discussions. [R454]

British pelagic tunicates. *J. H. Fraser. Published for the Linnean Society of London and the Estuarine and Brackish-Water Sciences Association by Cambridge University Press, New York, NY and Cambridge and London, U.K. Synopses of the British Fauna (New Series) No. 20 edited by Doris M. Kermack and R. S. K. Barnes. 1982. vii + 57 p. $12.95 U.S.* A concise account of the pelagic tunicates (Appendicularia and Thaliacea) found in British waters including keys for identification as well as sections on systematics and general biology — general structure and feeding, life history, locomotion, ecology, and distribution. [R455]

Laboratory manual for identification of ichthyoplankton from the Beverly–Salem Harbor Area. *Elaine Elliott and Doris Jimenez. The Commonwealth of Massachusetts, Department of Fisheries, Wildlife and Recreational Vehicles, Division of Marine Fisheries* (Cat Cove Marine Laboratory, 92 Fort Avenue, Salem 01970). *1981. 230 p. Free.* An up-to-date atlas of western Gulf of Maine ichthyoplankton. The manual combines pertinent literature on resident and nonresident species and supplements this with the authors' personal observations. Species are listed alphabetically by common name. Similarities among easily confused species are emphasized and key differences are noted. [R456]

Squid jigging from small boats. *Mototsugu Hamabe, Chikamasa Hamuro and Michio Ogura. Published by arrangement with the Food and Agriculture Organization of the United Nations by Fishing News Books Ltd., Farnham, Surrey, England. 1982. x + 74 p. £6.00 plus 60 p. post/packing.* This FAO Fishing Manual, edited by FAO Fisheries Technology Service, indicates an excellent potential for the creation of new fisheries. The authors, Japanese experts, share their knowledge and experience with other fishermen, researchers, and fishing technologists. Included are a general review of squid biology and behavior as well as descriptions of jigging equipment and aspects of handling, storage, and marketing. [R457]

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Potential secondary production from herring spawning in the Strait of Georgia
D. E. Hay and J. Fulton

Mercury uptake by lake trout, *Salvelinus namaycush*, relative to age, growth, and diet in Tadenac Lake with comparative data from other PreCambrian Shield lakes
H. R. MacCrimmon, C. D. Wren, and B. L. Gots

Average age at first reproduction of the northern fur seal **A. E. York**

Simulation of temperature and upwelling effects on the English sole (*Parophrys vetulus*) spawning season **G. H. Kruse and A. V. Tyler**

Tolerance and resistance to cadmium in white suckers (*Catostomus commersoni*) previously exposed to cadmium, mercury, zinc, or selenium
D. A. Duncan and J. F. Klaverkamp

Predicting the movements of juvenile Atlantic herring (*Clupea harengus harengus*) in the SW Bay of Fundy using computer simulation techniques
C. L. Jovellanos and D. E. Gaskin

Chemical and radiotracer measurements of phosphorus uptake by lake plankton
D. R. S. Lean and E. White

Factors influencing the size of lobster stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Maine: a new synthesis
G. C. Harding, K. F. Drinkwater, and W. P. Vass

Effect of fish size on the reactive distance of bluegill sunfish (*Lepomis macrochirus*)
J. E. Breck and M. J. Gitter

Lack of effect of arsenic on phytoplankton communities in different nutrient conditions
D. Planas and A. Lamarche

On density of chum salmon (*Oncorhynchus keta*) eggs in shallow matrix substrate incubators
A. R. D. Kapuscinski and J. E. Lannan

Factors affecting the relation between phosphorus and chlorophyll *a* in midwestern reservoirs
M. V. Hoyer and J. R. Jones

Mortality of starry flounders (*Platichthys stellatus*) with skin tumors **S. E. Campana**

Seasonal dynamics of the deep-chlorophyll maximum in Castle Lake, California
J. C. Priscu and C. R. Goldman

Salmon stock identification based on elemental composition of vertebrae
T. J. Mulligan, L. Lapi, R. Kieser, S. B. Yamada, and D. L. Duewer

Notes

Relationships among shelf temperatures, coastal sea levels, and the coastal upwelling index off Newport, Oregon **G. H. Kruse and A. Huyer**

Ammonia caused gill damage in channel catfish (*Ictalurus punctatus*): confounding effects of residual chlorine **S. J. Mitchell and J. J. Cech Jr.**

Letters and Comments/Lettres et commentaires: Misconceptions about estimating prey preference **H. A. Vanderploeg and D. Scavia**; Reply: Some pitfalls **S. Pearre Jr.**

Obituary/Nécrologie — Frank Harold Rigler, 1928–1982 **R. H. Peters**

Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments Supplement 1, 1983

Available from: Supply and Services Canada, Canadian Government Publishing Centre, Hull, Quebec, Canada K1A 0S9. (Canada $12.00, other countries $14.40)

Introduction to the Symposium on the Dynamics of Turbid Coastal Environments
D. C. Gordon Jr.

Modeling tidal stress, circulation, and mixing in the Bristol Channel as a prerequisite for ecosystem studies **R. J. Uncles**

Suspended sediment transport and deposition modeling in the Bay of Fundy, Nova Scotia — a region of potential tidal power development **D. A. Greenberg and C. L. Amos**

Factors affecting the supply and distribution of sediment in the turbid coastal environment **M. P. Kendrick and B. V. Derbyshire**

Supply, distribution, and transport of suspended sediment in a macrotidal environment: Bristol Channel, U.K. **M. Collins**

River-dominated suspended-sediment deposition in a new Mississippi delta **I. Ll. van Heerden, J. T. Wells, and H. H. Roberts**

Transfer of water and sediment from the Yangtze River to the East China Sea, June 1980 **Yang, Z.-S., J. D. Milliman, and M. G. Fitzgerald**

Distribution and behavior of fine sediment in the Severn Estuary and Inner Bristol Channel, U.K. **R. Kirby and W. R. Parker**

Characteristics of suspended cohesive sediment of the Severn Estuary, U.K. **R. Bryant and D. J. A. Williams**

Size of flocs suspended in Delaware Bay **R. J. Gibbs, L. Konwar, and A. Terchunian**

Modeling suspended sediment dynamics of the Miramichi Estuary, New Brunswick, Canada **G. V. Winters**

Turbidity maximum migration and harbor siltation in the Tay Estuary **C. Dobereiner and J. McManus**

Dynamics of coastal fluid muds in low-, moderate-, and high-tide-range environments **J. T. Wells**

The northern muddy intertidal: a seasonally changing source of suspended sediments to estuarine waters — a review **F. E. Anderson**

The mudflat coast of China **Y. Wang**

Optical properties, suspended sediments, and chemistry associated with the turbidity maxima of the Delaware Estuary **R. B. Biggs, J. H. Sharp, T. M. Church, and J. M. Tramontano**

Les flux de sels nutritifs dans l'estuaire de la Seine (France); rôle et importance du bouchon vaseux au cours du mélange estuarien **J.-F. Guillaud**

Behavior of nitrogen nutrients and silica in the Ems−Dollard Estuary **W. Helder, R. T. P. de Vries, and M. M. Rutgers van der Loeff**

Chemical composition of suspended particles in an estuarine turbidity maximum zone **D. H. Loring, R. T. T. Rantala, A. W. Morris, A. J. Blake, and R. J. M. Howland**

Sediments and metal pollutants in a turbid estuary **M. F. C. Thorn and T. N. Burt**

Heterotrophic bacterial biomasses, activities, and productivities within the Fraser River plume **L. J. Albright**

Vertical mixing and its effects on phytoplankton growth in a turbid estuary **R. J. Uncles and I. R. Joint**

Primary production and respiration in pelagic and benthic communities at two intertidal sites in the upper Bay of Fundy **B. T. Hargrave, N. J. Prouse, G. A. Phillips, and P. A. Neame**

Spatial and temporal variability of dinoflagellate cyst abundance in a tidal estuary **W. M. Balch, P. C. Reid, and S. C. Surrey-Gent**

Stable carbon isotope studies on the Pecks Cove mudflat ecosystem in the Cumberland Basin, Bay of Fundy **P. Schwinghamer, F. C. Tan, and D. C. Gordon Jr.**

Suspended particulate loading on the macrobenthos in a highly turbid fjord: Knight Inlet, British Columbia **G. E. Farrow, J. P. M. Syvitski, and V. Tunnicliffe**

Relations between annual dredging activities, suspended matter concentrations, and the development of the tidal regime in the Ems Estuary **V. N. de Jonge**

Particle resuspension in the benthic boundary layer induced by flow around polychaete tubes **D. A. Carey**

Tidal current speed and production of benthic macrofauna in the lower Bay of Fundy **D. J. Wildish and D. Peer**

Effect of turbidity on the temporal and spatial utilization of the inner Bay of Fundy by American shad (*Alosa sapidissima*) (Pisces: Clupeidae) and its relationship to local fisheries **M. J. Dadswell, G. D. Melvin, and P. J. Williams**

Sediment mobility in the Severn Estuary and its influence upon the distribution of shorebirds **P. N. Ferns**

Development of an ecosystem model of a turbid estuary **I. R. Joint**

Concluding remarks of session chairmen at the Dynamics of Turbid Coastal Environments Symposium, I **A. J. Bowen**
Concluding remarks of session chairmen at the Dynamics of Turbid Coastal Environments Symposium, II **D. C. Rhoads**
Concluding remarks of session chairmen at the Dynamics of Turbid Coastal Environments Symposium, III **G. Evans**
Concluding remarks of session chairmen at the Dynamics of Turbid Coastal Environments Symposium, IV **P. J. Wangersky**
Concluding remarks of session chairmen at the Dynamics of Turbid Coastal Environments Symposium, V **H. Postma**
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Poster papers presented at the Symposium
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Canadian Journal of Fisheries and Aquatic Sciences

Guide for Authors

Content

We welcome manuscripts reporting significant new information in the broad fields of fisheries science and management, marine and freshwater ecosystems, and aquatic biota relevant to Canada. Manuscripts must not be submitted or accepted for primary publication elsewhere.

Manuscripts are selected for publication according to the extent and significance of new knowledge or ideas presented; preference will be given to those with experimental results that emphasize casual mechanisms underlying observed phenomena rather than pure description and fact. In general, manuscripts reporting fragments of research are unacceptable, as are those of mainly local interest.

Articles: Studies of broad scope that are original contributions to science.

Notes: Differ from articles on the basis of scope or completeness, rather than quality of research. They may report significant new knowledge arising from problems with narrow, readily defined limits, or important findings that warrant immediate publication before broader studies are complete. Notes should occupy no more than 3 printed (9 manuscript) pages.

Reviews: Detailed critical appraisals of broad areas of investigation, particularly those that have developed rapidly in recent years.

Perspectives: Essays of opinion or hypothesis on aquatic science of concern to the professional and layman. References are desirable; informal style is welcome.

Letters and Comments: Opinion on topics recently discussed in the *Journal*; preferred maximum length, 500 words.

Editorial Practices

The *Council of Biology Editors Style Manual* (4th ed. 9650 Rockville Pike, Bethesda, MD 20814) is used as the authority in matters of form. The standards for spelling are *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in Serial Sources for the Biosis Data Base (Bio-Sciences Information Service, Philadelphia, PA 19103). References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (4th ed. 1980) Spec. Publ. No. 12, American Fisheries Society. All measurements must be metric and in SI units.

Series titles should be avoided. An *abstract* is required for all manuscripts and should state concisely, in less than 250 words, what was done, found, and concluded. Up to 10 *key words* should follow the abstract.

Each manuscript is normally submitted to two referees. Contributors are encouraged to suggest names of potential referees.

Illustrations should be submitted in triplicate as either xerographic or photographic reproductions. One set of photographs will be required when the manuscript is printed. They should not be mounted, stapled, or clipped. Symbols, letters, and numerals must be neat, and at least 1.5 mm high when the illustration is reduced to column width. Letters and numerals should be made neatly with a printing device (**not a typewriter**) and be of such size that the smallest character will not be less than 1 mm high when reduced. Drawings should, when possible, be grouped to facilitate comparisons.

Proofs are sent to the author, who is responsible for correcting errors in typesetting. *Alterations to the content must be avoided.*

Fifty *reprints* are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent with the proofs). A charge of $44.00 per page is made for articles published. When submitting a manuscript, authors should state that their institution will accept this charge.

Checklist on Manuscripts

Attention to the following questions will expedite appraisals of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables and figures and the text, or within the text? Should some of the data be made available separately, in a data or manuscript report or at a data repository? If you use statistical analysis, are the statistics subordinate to the research? When probability statements are made, are only the statistical tests cited and unnecessary statistical tables excluded?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report? Does the *abstract* give the essentials of the new knowledge? Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data? Are generalizations on the *results* adequate? Are findings distinguished from inferences from them? Is *discussion* limited to interpretation and significance of the findings?

Journal canadien des sciences halieutiques et aquatiques

Guide des auteurs

Sujet

Les manuscrits comportant une information nouvelle et significative dans le domain général de la science halieutique et de la gestion des pêches, des écosystèmes marins et d'eau douce et des biocoenoses aquatiques pertinents au Canada sont les bienvenus. Ils ne devront pas avoir été soumis au acceptés pour publication dans d'autres périodiques de fonds.

Le choix des manuscrits pour publication se fait selon l'étendue et la signification des connaissances au idées nouvelles qu'ils contiennent; on donnera la préférence aux articles contenant des résultats expérimentaux qui mettent l'accent sur les mécanismes sous-jacents aux phénomènes observés plutôt qu'à une simple description ou énoncé de fait. En général, les manuscrits portant sur des fragments de recherche sont inacceptables, de même que ceux qui n'ont qu'un intérêt local.

Articles: Études d'une portée générale, constituant des contributions inédites à la science.

Notes: Se distinguent des articles par la portée et le degré d'achèvement plutôt que par la qualité des recherches. Elles peuvent signaler une connaissance nouvelle et significative découlant de problèmes étroitement limités et facilement définis, ou d'importantes découvertes qui méritent d'être publiées avant que des études plus vastes ne soient terminées. Les notes ne doivent pas dépasser 3 pages imprimées (9 pages de manuscrit).

Critiques: Appréciations critiques détaillées de vastes champs de recherche, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives: Essais portant sur une opinion ou une hypothèse relative aux sciences aquatiques qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Lettres et commentaires: Opinions sur des sujets récemment exposés dans le *Journal*. Longueur maximale préférable, 500 mots.

Dispositions générales

Le *Council of Biology Editors Style Manual* (4e éd. 9650 Rockville Pike, Bethesda, MD 20814) sert de guide quant à la forme de la présentation. Le *Webster's Third New International Dictionary* et *le Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Serial Sources for the Biosis Data Base* (BioSciences Information Service, Philadelphie, PA 19103). Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (4e éd. 1980) Publ. spéc. nº 12, American Fisheries Society. Toutes les mesures doivent être conformes au système métrique et en unités SI.

On devra éviter les *titres en séries*. Un *résumé* doit accompagner chaque texte et doit exposer brièvement, en moins de 250 mots, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé. Le résumé doit être suivi d'un nombre de mots clés ne dépassant pas 10.

Chaque texte est soumis d'ordinaire à deux arbitres. Nous encourageons les collaborateurs à suggérer les noms d'arbitres possibles.

Les *illustrations* doivent être soumises en triple, sous forme de reproductions xérographiques ou photographiques. Au moment de l'impression du manuscrit, il faudra produire une série de photographies. Ces dernières ne devront être ni montées, ni agrafées, ni retenues par trombones. Les symboles, lettres ou chiffres doivent se détacher avec précision et doivent mesurer au moins 1,5 mm de haut lorsque l'illustration est réduite à la largeur de la colonne. Les lettres et les chiffres devront être soigneusement composés à l'aide d'un appareil d'imprimerie (**machine à écrire exclue**); leurs dimensions seront telles que la hauteur du caractère le plus petit ne soit pas après réduction. Les dessins doivent, autant que possible, être groupés pour faciliter l'étude comparative.

L'auteur doit revoir les *épreuves* qu'on lui remet et en corriger les erreurs typographiques. Il doit éviter de changer le contenu du texte.

Cinquante *tirés à part* sont fournis gratuitement. Des tirées à part supplémentaires peuvent être achetés au moment de la publication. (Un bon de commande à cet effet accompagne les épreuves.) Les frais sont de 44.00 $ par page pour la publication d'articles. Quand un auteur soumet un manuscrit, il doit préciser que son institution accepte les frais.

Liste de contrôle pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et rédacteurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude? Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le même texte? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la recherche?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncé dans l'introduction?

Le *titre* est-il représentatif du contenu du rapport? Le *résumé* donne-t-il l'essentiel des connaissances nouvelles? L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème? La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données? Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions? La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Canadian Journal of Fisheries and Aquatic Sciences

Guide for typists preparing copy

Read "Guide for Authors" in the January issue of current volume of the *Journal*. When in doubt about how to type or arrange details follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize the first letter of each word. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

Type the title, the author's names and affiliations, related footnotes, the running head, the abstract with its bibliographic citation, and key words on the first page (see Appendix A). Number all pages beginning with the title page, including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Scientific Information and Publications Branch.

A detailed guide with appendices is available from the Scientific Information and Publications Branch.

Abbreviations: Abbreviations used frequently in the *Journal* are listed in Appendix B.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).

Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send one photographic reproduction and two photocopies (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write on the illustration itself. Also, type the captions in succession on a separate page.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expression, Equations and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to and ensure that dates and spelling are correct. Type the reference list, *double-spaced*, in the style used in the *Journal* (see Appendix E). Abbreviate names of journals according to *Serial Sources for the Biosis Data Base*.

Headings: If the levels of importance of heads and subheads are not apparent from their positions, identify each of them with an appropriate circled number or letter in the left-hand margin of the typed page: 1 or A for the highest level, 2 or B for the second level, 3 or C for the third level. Or include with your manuscript a typed list of heads and subheads, indented as necessary to indicate their relative importance.

Journal canadien des sciences halieutiques et aquatiques

Guide pour les secrétaires d'auteurs

Lisez le « Guide des auteurs » dans le numéro de janvier du volume courant du *Journal*. Si vous avez des doutes sur le façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21,5 × 28 cm (8,5 × 11 pouces). Si possible, employez un papier avec lignes numérotées en marge. Laissez toujours une marge d'au moins 2,5 cm.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour la première lettre de chaque mot. Pour les petites majuscules, employez les minuscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs, les renvois qui s'y rapportent, le titre courant, le résumé avec sa référence bibliographique et les mots clés (voir annexe A). Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie ainsi que deux copies lisibles à la Direction de l'information et des publications scientifiques.

Un guide détaillé y compris des annexes est disponible gratis de la Direction de l'information et des publications scientifiques.

Abréviations: Nous donnons à l'annexé B une liste d'abréviations communément utilisées dans le *Journal*.

Tableaux: Consultez une copie du *Journal* pour la composition des tableaux (voir annexe C).
Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés:*

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des entêtes et au-dessous des colonnes, rarement ailleurs. Ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

À l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge « Tableau — près d'ici ».

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir annexe C).

Illustrations: Envoyez avec le manuscrit une reproduction photographie et deux photocopies (ne dépassant pas 21,5 × 28 cm) de chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas sur l'illustration même. De plus, dactylographiez les légendes, dans l'ordre, sur feuilles séparées.

À l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge « Fig. — près d'ici ».

Équations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir annexe D).

Indiquez clairement tous les symboles. Épelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et la chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans le liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à *double interligne* dans le style en usage dans le *Journal* (voir annexe E). Abrégez les noms des périodiques suivants les *Serial Sources for the Biosis Data Base*.

En-têtes: Si la position de vos en-têtes et sous-en-têtes ne suffit pas à indiquer leurs niveaux d'importance, identifiez chacun d'exu par un chiffre ou une lettre encerclé à la marge gauche de la page dactylographiée: 1 ou A pour le niveau supérieur, 2 ou B pour le deuxième niveau 3, ou C pour le troisième niveau. Ou encore, transmettez avec votre manuscrit une liste dactylographiée d'en-têtes et de sous-en-têtes rentrés de façon à indiquer leur importance relative.

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